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Erratum

The cut for Figs. 16–21, p. 499 was reversed in printing. Transpose 15 and 21; 16 and 20; 17 and 19.

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Studies on the morphology of the Onagraceae
VII. Gayophytum ramosissimum

DONALD A. JOHANSEN

(WITH PLATE 1 AND SIXTEEN TEXT FIGURES)

The phylogenetic position and relationships of *Gayophytum* have long been as obscure as those of many another genus in the Onagraceae. The most that has been conceded is that the genus is close to *Epilobium* (Trelease 1894, Johansen 1929); recently its position has been greatly clarified through the elucidation of its chromosome numbers. In the present paper, it is proposed to present an account of megagametogenesis and embryogenesis in a representative species, *G. ramosissimum* Torrey & Gray, and to make certain comparisons aimed toward defining the phylogenetic position of the genus.

The genus is very poorly known, owing to the small size of most of the species, the insignificant flowers and the restriction of the various species in both North and South America to comparatively inaccessible portions of the high mountains. Extremely little has been contributed to our knowledge of the genus, or of any of its species, since Trelease's revision (1894). Most accounts which have appeared in the meantime, particularly those in floras, are drawn wholly from this source.

Gayophytum is represented in western North America by about nine species, with others in western South America. No species seems to be known from either Mexico or Central America: the reason for this gap needs to be explained by future monographers of the genus.

MATERIALS

Gayophytum ramosissimum is a widespread form, occurring from Washington easterly to Montana, thence south to Colorado and through Nevada and Arizona to California and down into Baja California as far as the Sierra San Pedro Martir. It does not seem to be known from Oregon. Material of no other species has thus far been procurable, hence it will be necessary to consider *G. ramosissimum* as typical of the genus in so far as phylogenetic considerations are concerned.

Two different collections from widely separated localities have been available for study. One lot was collected by Dr. Ira L. Wiggins on September 2, 1927 in open flats in a pine forest, at an altitude of about 6100 ft., in the Laguna Mts. of San Diego County, California. The other collection was secured by the writer on September 6, 1930 from plants growing along the roadside in a pine forest near the summit of Donner Pass in the Sierra

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Nevada Mts. of Nevada County, California, at an elevation of 7135 ft. *G. ramosissimum* is essentially a high-montane species, but is not an alpine plant. The two groups of material are identical morphologically and cytologically, hence in the descriptions and figures no distinction is being made.

The material collected by Dr. Wiggins was thoroughly studied during the same year that it was collected but not all stages were represented, and it was therefore necessary to postpone the completion of the study until the second lot of material was available.

OVARY AND OVULES

The ovaries of *G. ramosissimum* resemble those of that group in the genus *Epilobium* represented by *E. paniculatum* but are biloculate and the number of ovules to each loculus averages six. The ovules regularly alternate in the adjoining locules.

The ovules are rather small, as are the mature seeds. The nucellus is of slight extent; although not attacked to any appreciable extent by the developing megagametophyte, it nevertheless has completely disappeared by the time the embryo has completed growth. Both a hypostase and an epistase are present; the latter originates almost simultaneously with fertilization, hence appears far earlier than it does in any other onagrad known to us.

In practically every older ovary there are generally to be found quite a few aborted ovules. The sterility of these ovules seems to be due to only two causes. One is the failure of the functioning megaspore to continue growth once it becomes started. This phenomenon has been observed repeatedly. The other cause is a unique one: after the second division in the young megagametophyte, the three upper groups of chromosomes, which should form the egg nucleus and synergid nuclei respectively, are unable to reconstitute themselves into nuclei but become clumped together and finally break down completely (Pl. 1, fig. 15). This phenomenon, when first noticed, was naturally thought to be evidence of poor fixation, but careful study of a large number of cases at all stages finally revealed the true explanation. We had previously observed the same thing in other genera (e.g., *Taraxia ovata*, *Zauschneria latifolia*, etc.) but were not then aware that it was of any significance as a cause of ovular sterility.

MEGAGAMETOGENESIS

The megagametophyte originates in the fashion typical for the family, and its growth into the quartet is likewise typical. In the Donner Pass material we frequently found metaphases and anaphases of the first division, but the excessively small size of the chromosomes precluded, in

most cases, the making of accurate counts. In Plate 1, fig. 1, is shown a clear diaphase figure with eleven bivalents. The extremely small size of the anaphase chromosomes can be seen in Plate 1, fig. 2. Here, too, there are eleven elements and the split for the second division is already evident. The chromosomes preserve their identity during the interphase (Pl. 1, fig. 3); several such stages have been encountered and in most of them it was possible to count eleven chromatin blobs which were distinctly constricted in the center, exactly as in the anaphase figure.

The micropylar megaspore of the quartet (Pl. 1, fig. 4) is always the functional one (Pl. 1, figs. 5, 6).

The plane of the first division in the young megagametophyte is either transversely or longitudinally situated; the latter position is the normal one among onagrads. There seems to be some evidence that the nuclei resulting from a transversely placed division figure do not later become oriented one above the other, as not infrequently happens in other onagrads, but divide while still in the positions first assumed, and the spindles of the second division are irregularly oriented as a consequence. In this probably lies the explanation of the erratic organization of many megagametophytes.

The mature megagametophyte most commonly observed is similar to the one portrayed in Plate 1, fig. 9. This type plainly shows the effects of an inadequate water supply. A well organized megagametophyte is not often found (Pl. 1, fig. 10); the synergids are well indented and each possesses a rather fragile so-called filiform apparatus that easily collapses and disappears. The egg cell is comparatively small and the polar nucleus is much less prominent than in other onagrads. In many well nourished megagametophytes the synergids and egg cells contain much starch, and in some embryo sacs which were especially well nourished, the megagametophytes were heavily gorged with starch grains of a large size.

FERTILIZATION

All the stages of syngamy, as well as the fusion of the secondary male nucleus with the polar nucleus, have been observed. The entire process in each union does not differ in any manner from the descriptions for other species already presented. Plate 1, fig. 11, shows a stage rarely found, and it is one which we have hitherto not been able to figure. The primary male nucleus is in the very act of entering the neck of the egg cell, while the secondary male nucleus is in the megagametophytic cytoplasm (to the left of the egg cell), on the way down to meet the polar nucleus. Plate 1, fig. 13, shows a middle stage of syngamy, while figure 14 shows a corresponding stage in the union of the secondary male nucleus with the polar nucleus.

During fertilization there can sometimes be found in the upper part of the embryo sac many globular bodies having the staining reaction of chromatin; they are similar to those described in *Zauschneria latifolia* (Johansen, 1931), but we could not ascertain anything about their origin.

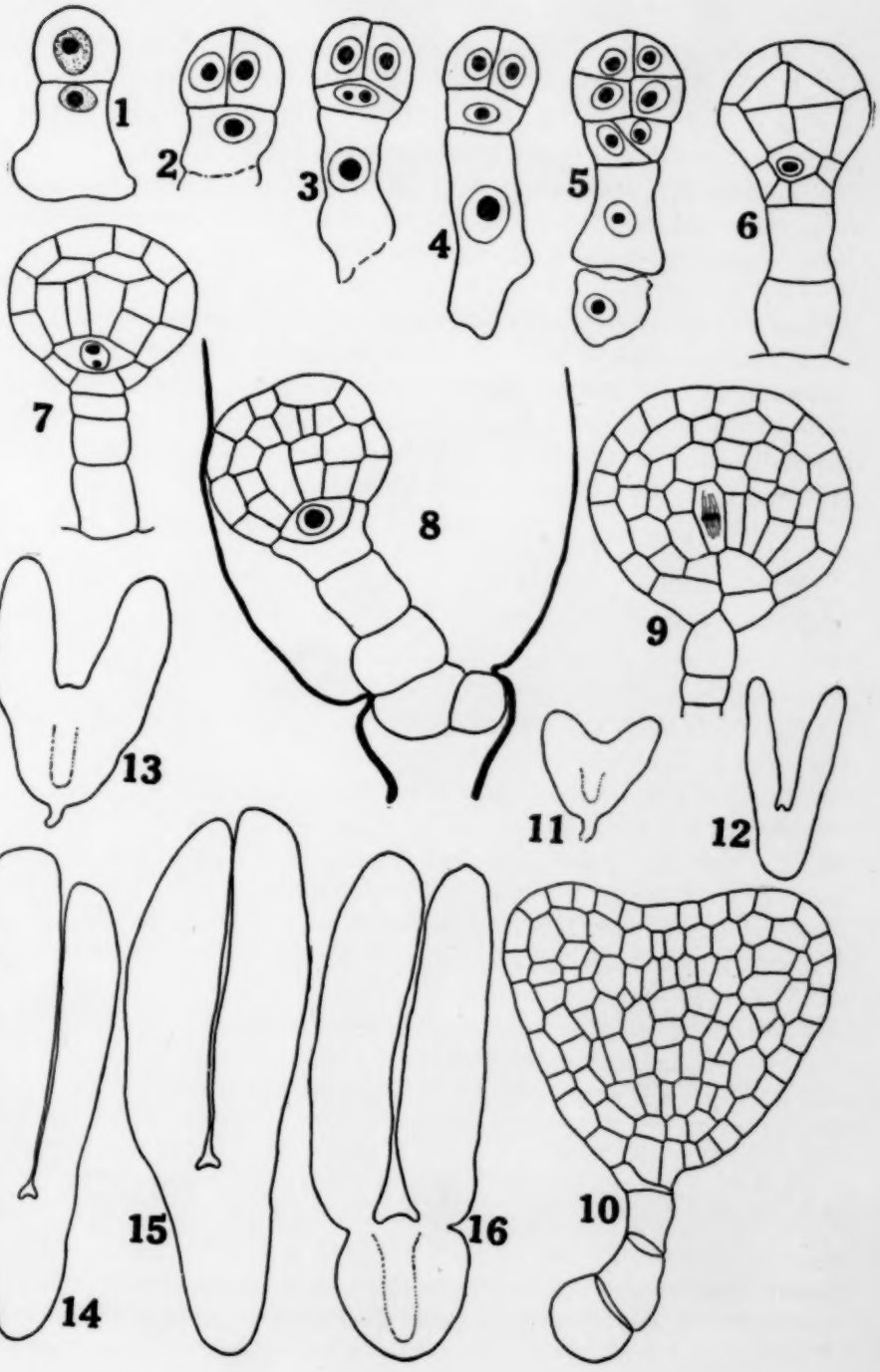
EMBRYOGENESIS

For some obscure reason, the zygote delays division for a long time. The earlier divisions are typical (text figs. 1–4). The suspensor initial cell may become much elongated (fig. 4) before it is transversely split into two or more unequal cells (figs. 5–7). The suspensor of this species is, in fact, far more persistent despite its small size than in the species in other genera which have suspensors of similar size and construction. It has even been observed to grow out into the tapetal portion of the ovule (into the channel left by the microgametophyte) and to become wedged in the opening in such a manner that the young embryo literally appears as if suspended in the embryo sac by its suspensor (fig. 8).

The hypophysis cell in *G. ramosissimum* behaves rather inconsistently, and it is for this reason that the radicle cannot always be clearly delimited in mature embryos. An examination and comparison of figures 5–9 will bring out this point. In figure 5 an oblique wall divides the hypophysis initial; a second oblique wall will presently be formed in the cell to the right and by a division in the cell at the left this wall will apparently be continued through to the opposite outer wall. Figure 6 shows the result of this method of origin of the root-tip (still only one cell in extent) and the root-cap. In figure 7 we have the usual representation of the earlier divisions in the hypophysis initial. In figure 8 the hypophysis cell has divided in the characteristic manner but no walls have yet been erected in the lower cell, which gives rise to the root-cap tissues.

The later developmental stages are wholly typical. Mature embryos are almost exact duplicates of the normal embryos (*Type A* embryos) of *Zauschneria latifolia;* e.g., compare figures 14–16 of this paper with figures 67–69 of the latter species in a former paper (Johansen 1931). In the oldest embryos, organization of the various tissues is the most regular and symmetrical that we have yet encountered in the Onagraceae.

Figs. 1–16. Embryogenesis. Except where noted, the magnification is 950. 1. Two-celled stage. 2. Three-celled. 3. Quadrant stage. 4. Quadrant with elongated suspensor cell. 5. Octant. Notice oblique division in hypophysis cell. 6, 7. Later stages. 8. Embryo whose suspensor has grown into the channel left by the microgametophyte. As the embryo actually hangs downward in nature, the figure should be reversed for a more accurate conception of its position. 9. Globular stage. 10. Beginning of cotyledon development ×475. 11–13. Stages in cotyledon development. ×120. 14–16. Latest stages in development. ×120.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ENDOSPERM

The polar nucleus takes up a position at the center of the embryo sac (Pl. 1, figs. 9–10). Following the first division after fusion with the secondary male nucleus, the two resultant nuclei remain at the center but not close together. After the second division, two nuclei remain at the center, while one nucleus moves to the vicinity of the egg cell and the fourth goes to the extreme chalazal end of the embryo sac, as shown in Plate 1, fig. 12. Later divisions were not followed out.

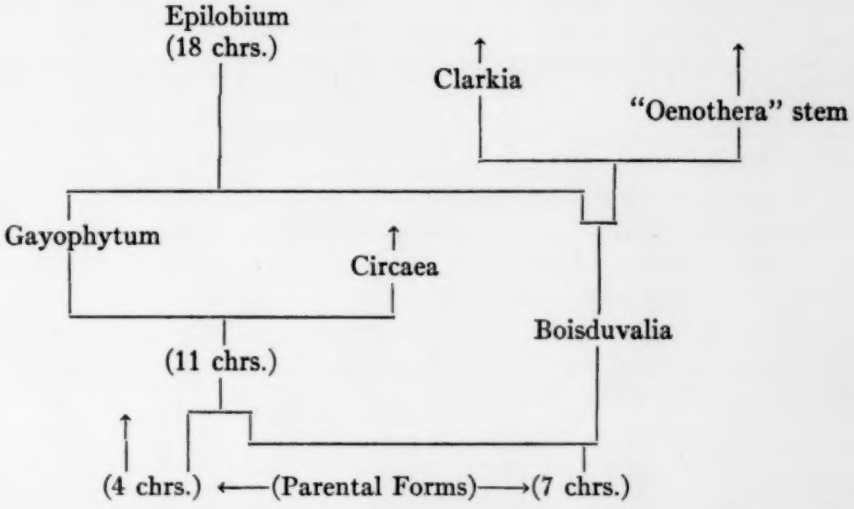
The "endosperm" nuclei rarely total over twenty and all vestiges have disappeared by the time the embryo approaches maturity.

The division figures in the "endosperm" are exceptionally clear in *G. ramosissimum*. Mitoses are generally simultaneous in any given ovule, while in the majority of other genera they commence at the micropylar end of the sac, progressing towards the opposite end. Many counts have been made and the number (diploid) was always 22.

THE PHYLOGENETIC POSITION OF GAYOPHYTUM

As explained in the opening paragraph, *Gayophytum* is taxonomically most closely related to *Epilobium*. The cytological evidence of the relationship, however, is at first contradictory because the basic number of chromosomes in the one is 11 and in the other 18. It has already been suggested that *Epilobium* should be considered as of hybrid ancestry (Johansen 1929), but until now the position of *Gayophytum*, whether above or below *Epilobium*, has remained doubtful. Recalling that the family presumably originated from two forms, one of which possessed 4n chromosomes, the other 7n, and that a cross between the two parental forms would reasonably have 11n chromosomes, we immediately obtain a good basis for speculation. Genetical studies on other plants have previously shown that the result when a cross is in one direction is not always the same when the cross is reciprocal. We are evidently dealing with a similar cross here, since we already have a series in which the basic number of chromosomes is 11 (*Circaea*, *Lopezia*, *Fuchsia*, etc.) but to which *Gayophytum* shows no systematic relationship. From the crosses between the two parental forms, in other words, two phylogenetic lines arose. One of these begins with *Gayophytum* and, so far as our present knowledge goes, also stops there. To complete the chain of evidence placing *Gayophytum* below *Epilobium* phylogenetically and to demonstrate further that the former is one of the parents of the latter, we have but to find the other presumable parent of *Epilobium*. Certain taxonomists have expressed a mild opinion that some sort of relationship exists between *Epilobium* and *Boisduvalia*. (The latter genus is directly derived from the 7n chromosomal ancestor.)

To sum up a strong probability, *Epilobium* represents a hybrid between *Gayophytum* and *Boisduvalia*. A diagrammatic representation of the idea may assist in making it clearer:



It might be profitable to examine some of the evidence underlying the assumption outlined above. First, the cytological evidence is in agreement, and incidentally all three genera concerned have very tiny chromosomes. Second, there is considerable morphological evidence, much of which has not yet been published. It is unfortunate that the few accounts of the embryology of *Epilobium* are so fragmentary as to be valueless. The writer's own investigations on several species in this genus reveal that embryogenesis differs greatly among different species; that is, there are so many divergencies in various details that a single description will hardly cover the entire genus. The embryos of *E. californicum* and *E. lanceolatum*, for example, differ much in size and in the latter species the behavior of the hypophysis cell is peculiar. Nothing has been published on *Boisduvalia*, but *B. campestris* and *B. densiflora* have been studied to some extent. Sufficient is known of the embryology in all three genera, in any event, to warrant the statement that the embryology of *Epilobium* is essentially a fusion of that of *Gayophytum* and *Boisduvalia*, some species resembling peculiarities in one of the latter genera, others those of still other species.

SUMMARY

1. The phylogenetic position of *Gayophytum* has been so obscure that an attempt was made to solve the problem on the basis of cyto-morphological data.

2. In the representative species studied, *G. ramosissimum*, the ovaries are biloculate, with an average of six ovules to each loculus.

3. The nucellus is of slight extent and disappears early during growth of the embryo.

4. Two causes of ovular sterility are described.

5. Megagametogenesis is typical; the micropylar megaspore is the functional one.

6. The embryology is fairly regular. No apomictic structures have been encountered.

7. The chromosome numbers are n-11, 2n-22. These indicate that the genus arose as a cross between the two parental forms of the family.

8. *Gayophytum* is one parental form of the hybrid genus *Epilobium*, the other presumably being *Boisduvalia*.

The greater part of this study was prosecuted during the tenure of a National Research Council Fellowship in the Biological Sciences, with residence at Stanford University.

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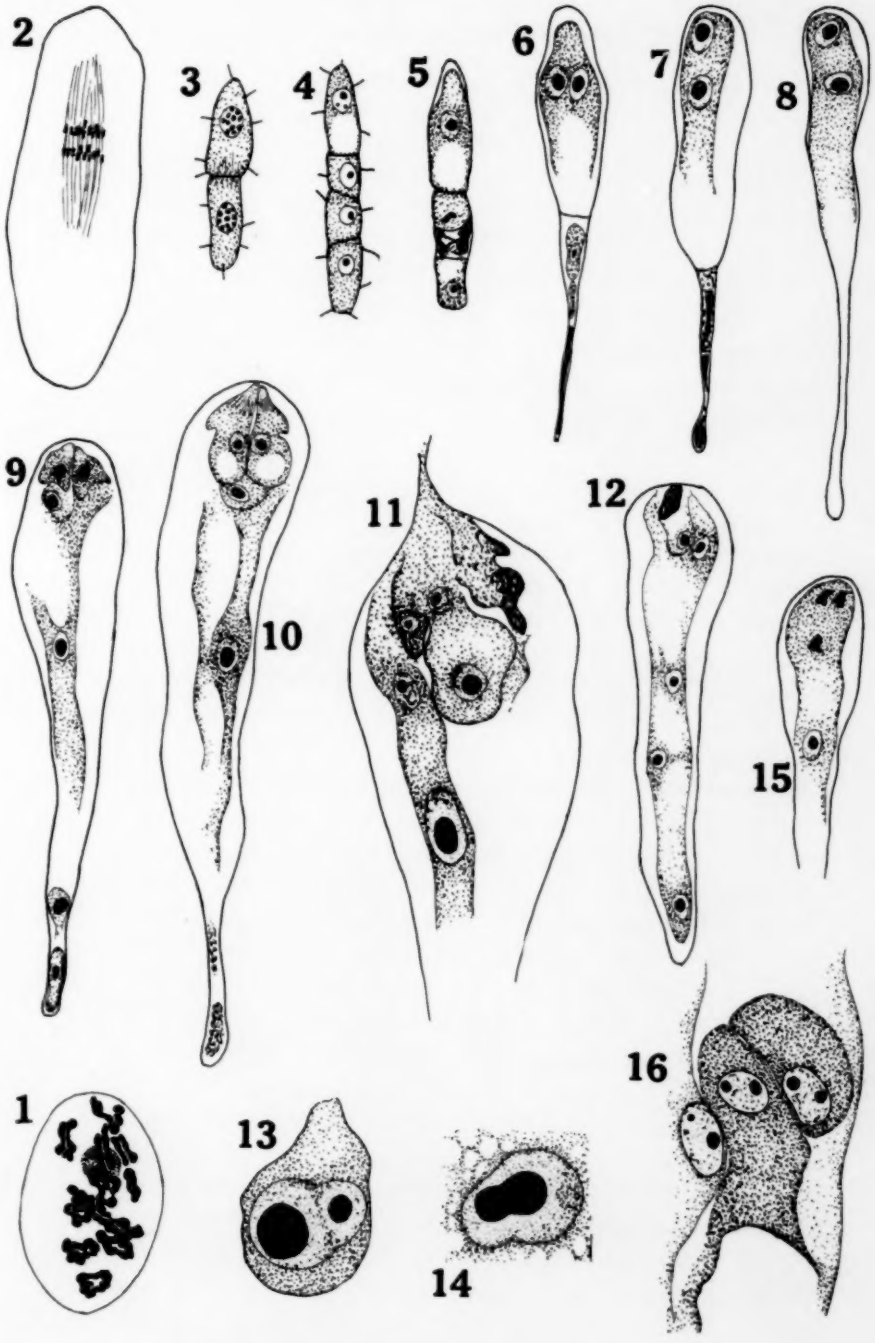
Trelease, W. 1894. Revision of the North American species of *Gayophytum* and *Boisduvalia*. Ann. Rep. Missouri Bot. Gard. **5**: 107–122.

Explanation of plate 1

Figs. 1–16. 1. Diaphase from megasporocyte, eleven bivalents. ×1250. 2. Anaphase of first division in megasporocyte. ×475. 3. Interphase. ×475. 4. The quartet. ×475. 5. Beginning of growth in the functioning megaspore. ×475. 6–8. Binucleate megagametophyte, the first figure with the nuclei oriented side by side, the other two with these nuclei one above the other (normal position). ×475. 9. Type of mature megagametophyte usually found. ×475. 10. Well nourished megagametophyte, showing regular organization. ×475. 11. Fertilization. Primary male nucleus in neck of egg cell; secondary male nucleus to right of egg cell. One synergid nucleus is between the two male nuclei. ×950. 12. Disposition of "endosperm" nuclei after second mitosis. Zygote shows no sign of approaching division. ×475. 13. Syngamy. ×1250. 14. Fusion of secondary male nucleus with polar nucleus. ×1250. 15. Typical instance where nuclei were not organized at micropylar end of megagametophyte after second division in latter. ×950. 16. False "embryo" in endosperm; it had six "cells" altogether. ×1250.



JOHANSEN: ONAGRACEAE

UNIV. OF MICH.

Crown gall on Sahuaro (Carnegiea gigantea)[1]

MICHAEL LEVINE[2]

(WITH PLATES 2, 3)

Up to the present time the crown gall disease has been unknown on any member of the Cactaceae. Smith (1911) reported the effects of inoculation of a poplar strain of *Bacterium tumefaciens* on four varieties of Opuntia. In only one case was a small "tumor" formed four months after inoculation which regressed eight months afterwards. No sections of this material were reported. The so-called grape strain of *B. tumefaciens* gave no results when the opuntia was inoculated with it. It appears that up to the present, no complete evidence has been presented to show that the Cactaceae react to the crown gall organism.

Smith (1922) contended further, that fasciations can be produced in *Nicotiana*, *Pelargonium*, *Ricinus*, *Brassica*, and *Tropaeolum* by inoculations with *B. tumefaciens*. Fasciations, he believed, result from disturbances due to the penetration of a foreign organism into the growing point. This causes crowding and division of the growing point or brings about irritations which lead to fusions. Shreve (1931) believes that fasciations in cacti, "cristates" as they are called, are not the results of fungi or bacteria but are probably due to a mechanical injury induced by a foreign substance introduced by an insect. *B. tumefaciens* or strains of this organism have not been isolated from the cacti. The existence of cristates suggests such a possibility and further study on these structures is needed.

The importance of having material for crown gall study available at all times has led me to investigate a number of species of Opuntia. The common house and garden plants commonly used in laboratories for crown gall studies, require much attention. They grow old, woody, shed their leaves, and become quiescent after they are transferred from the garden to the laboratory, which makes them unavailable subjects of experimentation for a number of months. The other disadvantage in the use of the ordinary plants lies in the rapid development of the tumor so that the progress of the growth cannot be studied with great detail. The cacti so far studied are not suitable for testing the virulence of various strains of *B. tumefaciens* because of the slow development of the tumor.

It is generally accepted in all tumor work, animal and plant, that the younger the host the more rapid is the response and the greater is the development of the new growth. From this point of view, it appeared to be

[1] Completion made possible by a grant-in-aid from the Chemical Foundation.

[2] Laboratory Division, Montefiore Hospital, N. Y.

of interest to determine what happens to the Sahuaro when subjected to an inoculation with a virulent strain of *B. tumefaciens*. MacDougal (1926) pointed out that the cells of the Sahuaro show individual activity for periods over a century. This view is apparently correct for the study reported below shows comparatively old cells capable of producing neoplastic responses which have not been obtained in tissues of other plants of similar or younger age. Then again, it is of importance to determine, in view of the reported long period of individual activity of these cells, whether or not the new formation on this tree-cactus would behave like the galls on other plants. The observations of the present writer (Levine, 1931) led him to the conclusion that the cells of the crown gall tissue are at first embryonic in nature but soon become differentiated, mature, and die. It was of interest to study the behavior of the cells in Sahuaro tumors.

Without resorting to field material it is impossible to inoculate the very old tree-cacti, but by inoculating the side ridges of small Sahuaros, approximately five to six years of age, it is possible to study the reaction of much older tissue than one can obtained by inoculating the growing shoots of the leafy plants generally used for crown gall study. The age of the growing shoots of the latter may be but a few days to a week old, while the cells along the ridges of the Sahuaro may be over a year old. According to Britton and Rose (1920, p. 164) Shreve states that the Sahuaro, at the age of eight to ten years, is only four inches tall. It is estimated (Shreve, 1931) that the rate of growth in larger plants is about four inches a year. Growth in these young plants is very slight, so that at the age of thirty years they are only three feet tall.

MATERIAL AND METHODS

In the fall of 1926 a large number of young joints of Opuntia were sent to me through the courtesy of Dr. D. T. MacDougal from southern United States, Mexico, and South America. A collection of joints[3] already rooted, were furnished me by the New York Botanical Garden. These plants were set out under favorable conditions in the laboratory where an abundance of sunlight was present for the major portion of the day. In April, 1931, a dozen Sahuaro plants from Arizona were sent to me by Dr. MacDougal These were wrapped in cotton and were somewhat shriveled when they reached New York. These plants were potted and set out in the greenhouse under favorable conditions until they struck roots.

Some Opuntia joints were cut aseptically and placed in large sterile culture dishes and then inoculated by covering one cut surface with one of

[3] *Opuntia Keyensis, O. Dillenii, O. stricta* and *O. Linderheimeri* were furnished me through the courtesy of Dr. N. L. Britton, to whom I owe my sincere thanks.

two strains of *B. tumefaciens*, used at that time in my laboratory. The rooted plants were inoculated in the usual way. Tumor tissue which developed was removed from the plant without disturbing the rest of the growth, while in other instances, a longitudinal section was made to pass through the medium portion of the gall and the plant. Sections of the tumor tissue including normal parts of the plant, were fixed in Bouin's and Flemming's weaker solutions. The material was imbedded in paraffin and serial sections 7.5μ to 10μ in thickness were cut. These were stained in Flemming's triple stain or in Heidenhain's iron haematoxylin.

OBSERVATIONS

The Opuntia

The Opuntia, as well as the Sahuaro, when inoculated with a virulent strain of *B. tumefaciens* produces first, an area of necrosis. This area, it would seem, is most apparent in plants that respond slowly to the inoculation of the bacteria. This necrotic area is also present in the sections of joints prepared in culture dishes. No reaction followed in these sections for a period of over three months. Then however, the pieces of the cactus began to disintegrate and became invaded by moulds. No reactions were found similar to those reported by Smith (1911) for sections of turnips or Blumenthal and Hirschfeld (1917), and Magnus (1918) for sections of carrots. The rooted joints of the Opuntias, in most cases, produce comparatively large areas of necrosis which become progressively brown and then black in color and finally harden, leaving a small depression in the region of inoculation. Sections through these areas show compact tissue below the necrotic area in the nature of a callus. Invariably, these sections show invasion of hyphal strands. In no instance was a well-formed tumor mass formed on the Opuntias studied, yet new joints were formed by tissues adjacent to the region of inoculation.

The Sahuaro crown gall

Tumors on the Sahuaro are formed after inoculation with a virulent strain of *B. tumefaciens*, introduced into the tissue by the aid of several pricks of a needle which had been previously immersed in a sub-culture of the organism. As in the Opuntias, the first reaction to the inoculation is the formation of a small blackened area around the needle pricks. This, it would seem, is due to the destruction and death of the seriously injured cells. The development of the tumor tissue in this cactus is relatively of long duration as compared with the reaction of the common plants generally used for the experimental study of this type of tumor. The necrotic areas induced in these plants persist for a long time also. In such plants

as the tomato, sunflower and the castor bean, the necrotic area persists for a short time and new formations may be detected in actively growing plants within a few days. I have studied sections of the early stages in tumor formation in connection with another problem which is under investigation, and found active cell proliferation in the tomato and sunflower within two to three days after inoculation.

In the Sahuaro the necrotic area persists for over a month or more, but is soon followed by the development of small pale-green modules on one side of the destroyed tissue; or they may arise from cells below the dead tissue. Two or several coalescing nodules may form simultaneously at the region of inoculation. The nodules are very small at first, but grow comparatively fast. The first photograph of these nodules was made six months after inoculation. An average tumor at this age is shown in figure 1. The largest gall formed is approximately 15 mm while the smallest is about 3 mm to 4 mm through its largest diameter. A tumor eleven months old is shown in figure 2. Fourteen months after inoculation, the largest gall measured 2 cm to 3 cm as shown in figures 3 and 4. It must be borne in mind that the tallest Sahuaro in my collection at this time, measures 8 cm to 10 cm above the soil.

These tumors on the Sahuaro are old galls chronologically when compared with tumors on the other flowering plants generally used for this study. Yet they are soft and section readily as pointed out below. A well-formed gall on the rubber tree, *Bryophyllum* or any other perennial plant so far studied, is filled with whorls of woody tissue and cork, making a microscopic study of this tissue by the usual means, impracticable.

The tumors on the Sahuaro, as those on other plants, are smooth and resemble more closely tumors found on the garden beet, *Beta vulgaris*. They are usually sessile and surrounded by host tissues, as shown in figure 4; or they may have a short, thick stalk, as shown in figure 3. In this figure it is of interest to note that a layer of epidermis has formed on one side of the gall containing a large number of densely set areoles with numerous spines. This would be comparable to the leafy shoots frequently found on galls of tobacco, and less commonly on the geranium and Jimson weed (*Datura stramonium*).

Histology of the Sahuaro tumor

Nodules of several tumors were studied in long serial sections. As noted above, the tumors fix readily in Bouin's and Flemming's weaker solution and present beautiful sections for microscopic study when stained with Flemming's triple mixture. Large pieces of the tumor tissue were prepared so as to give a complete picture of the histology of the tumor.

The tumor tissue is made up of parenchymatous cells interspersed with numerous areas of more actively growing, undifferentiated cells. Whorls of cells composed of protoxylem with well-formed tracheids are abundant.

In a section of a young nodule such as that shown in figure 6, two distinct areas may be observed; the peripheral portion, which is made up of small embryonic-like cells, and the larger interior portion, made up of larger and maturer cells. Figure 6 represents a longitudinal section through one of the nodules shown in figure 2. The surface or periphery of the small tumor mass consists of several layers of embryonic-like cells mentioned above. These cells show a comparatively large nucleus imbedded in a homogeneous densely granular cytoplasm. No evidence of an epidermis and palisaded layers of cells is present. Necrotic cells are found adhering to the surface of the peripheral layer of the tumor. The interior parenchymatous cells are of various sizes, due probably to sections of these cells whose polarity has been disoriented. The cytoplasm of the parenchymatous cells consists of a coarse reticulum made up of extremely fine granules as shown by MacDougal (1926). In sections of larger tumors, such as shown in figure 4, abundant clusters of protoxylem cells appear in the tissue, as shown in figure 7. They consist of elongated, cylindrical cells with small nuclei and dense cytoplasmic material. In some sections of this tissue, spiral tracheids may be seen in the process of development.

I have been unable to find early stages in nuclear division in the peripheral or parenchymatous cells of this tissue. Chromosome counts of the cells of this tumor would be of great interest. Late stages of nuclear and cell divisions are common, however. In the older cells, starch grains are abundant while in the young cells, such as shown in figure 6, they are entirely absent.

I have studied the slime or mucilage cells in the host tissue and searched the tumor material for similar structures. In none of my tumor tissue on this plant have I been able to find evidence of the presence of these cells. The mucilage cells, while not present in the tumor tissue, appear to be more abundant in the host tissue adjacent to the tumor. Figure 8 is a section through a gall shown in figure 4. The photograph represents the area of the tissue lying between the host and gall tissue. The area to the upper right in the figure represents gall tissue. The rest of the figure represents host tissue. The host tissue is characterized by a large number of the mucilage cells which are evidently very abundant below the base of the tumor tissue. The presence of these cells, it seems, may also serve as a defense mechanism. It appears that the injury which induced the crown gall tissue may have indirectly stimulated the formation of a larger number of slime cells than usual. The absence of these cells in the crown

gall tissue may be associated with the age of the gall. It is possible that in still older neoplasms of the Sahuaro, mucilage cells may be found. Sections of normal portions of the tree-cactus show a preponderance of mucilage cells forming a zone below the palisade layer, while they are less frequent in number towards the middle portion of the plant.

The mucilage cells of the Sahuaro are larger than the cortical cells of this plant. Frequently, two or more cells seem to fuse, forming a large mass of mucilage as shown in the upper left of figure 8. This may have led to the idea that mucilage forms in inter-cellular spaces as maintained by earlier workers. My observations of the formation of mucilage cells lead me to concur with the views of Miss Stewart (1919) that the slime and mucilage cells are a product of the cytoplasm and nucleus. As the slime increases in the cell, the cytoplasm and nucleus are crowded into a smaller space until the protoplasm of the cell completely disappears. My figures of old mucilage cells show rather constantly the presence of a diffusible substance on the periphery of the mucilage cell which permeates the surrounding cells. The substance stains a deeper gentian violet than the stratified mucilage, as shown in figure 9. The significance of this zone about the mucilage cell is not clear.

I wish to express my sincere thanks to Doctor D. T. MacDougal, who through a period of six years, has furnished me with various species of cacti and whose advice has been a great stimulus to me.

SUMMARY

1. As far as the crown gall literature is available, it appears that crown gall disease on the Sahuaro (*Carnegiea gigantea*) is reported here for the first time.

2. The tumors on this plant were induced by inoculations with *B. tumefaciens*.

3. Sections of these growths show structures which are analogous to crown gall tissue on other flowering plants studied.

4. The tumors on the plants reported here are the oldest (chronologically) crown gall tissues so far studied microscopically.

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Explanation of plates 2, 3

The photomicrographs were made with Zeiss 35 cm. camera.

Fig. 6 was made with the aid of Zeiss Obj. 6 and oc. K 3 bellows 25 cm.

Figs. 7–9 were made with the aid of Zeiss Obj. 10 and oc. K 10 bellows 25 cm.

Fig. 8 was made with the aid of Zeiss microplanar 3.5 cm. and bellows 50 cm.

Fig. 1. Sahuaro inoculated with *B. tumefaciens* 6/13/31, photographed 12/13/31 showing small tumor at point of inoculation. ×1/2.

Fig. 2. Another plant showing three fused tumor masses eleven months after inoculation. ×2.3.

Fig. 3. Smooth globular tumor with clusters of areoles and spines 13 months after-inoculation. ×1.

Fig. 4. Rough warty crown gall showing necrotic area.

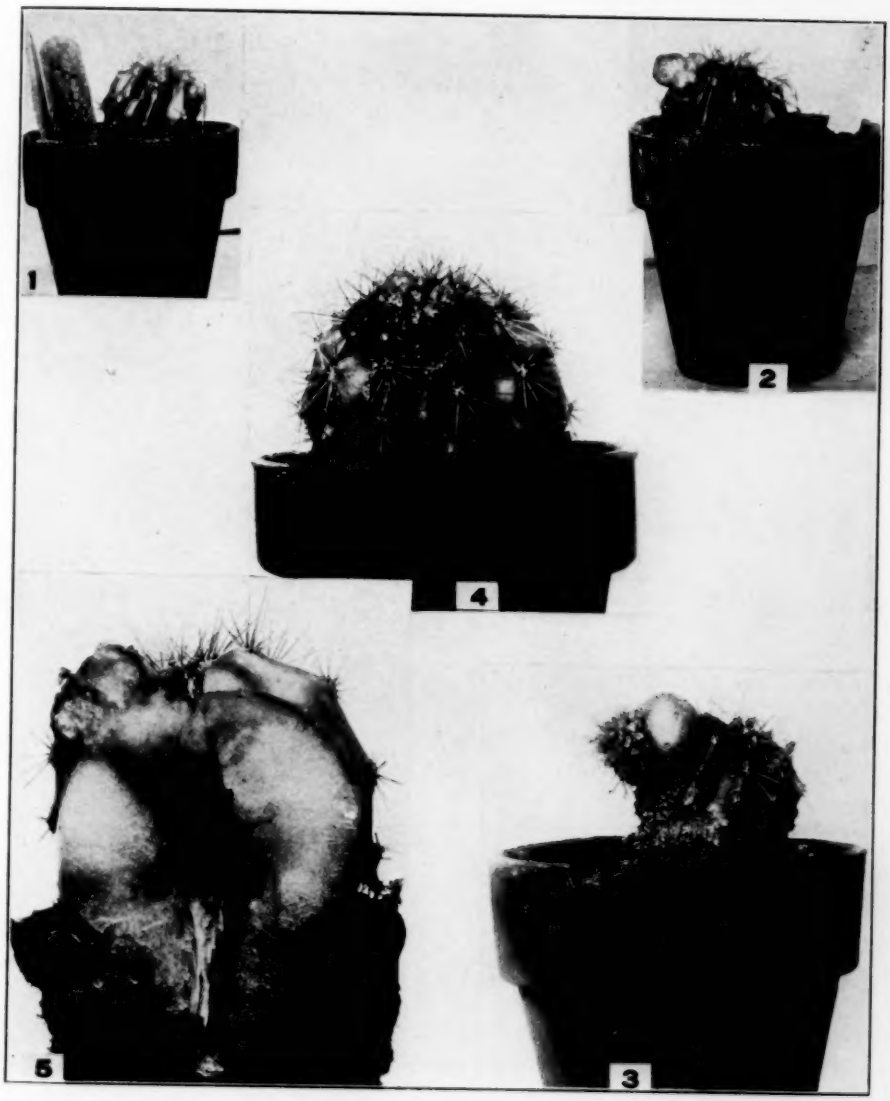
Fig. 5. Longitudinal section of the plant shown in fig. 4. Note attachment of sessile tumor.

Fig. 6. Longitudinal section of the nodule of the tumor shown in fig. 2. Note small size of peripheral cells; no mucilage cells.

Fig. 7. Section of tumor showing protoxylem cells.

Fig. 8. Longitudinal section through tumor shown in figs. 4–5. Note distribution of mucilage cells below base of tumor in a region distinctly host tissue.

Fig. 9. Enlarged portion of a section of fig. 7. Note the halo of the diffusible substance about the mucilage cell.



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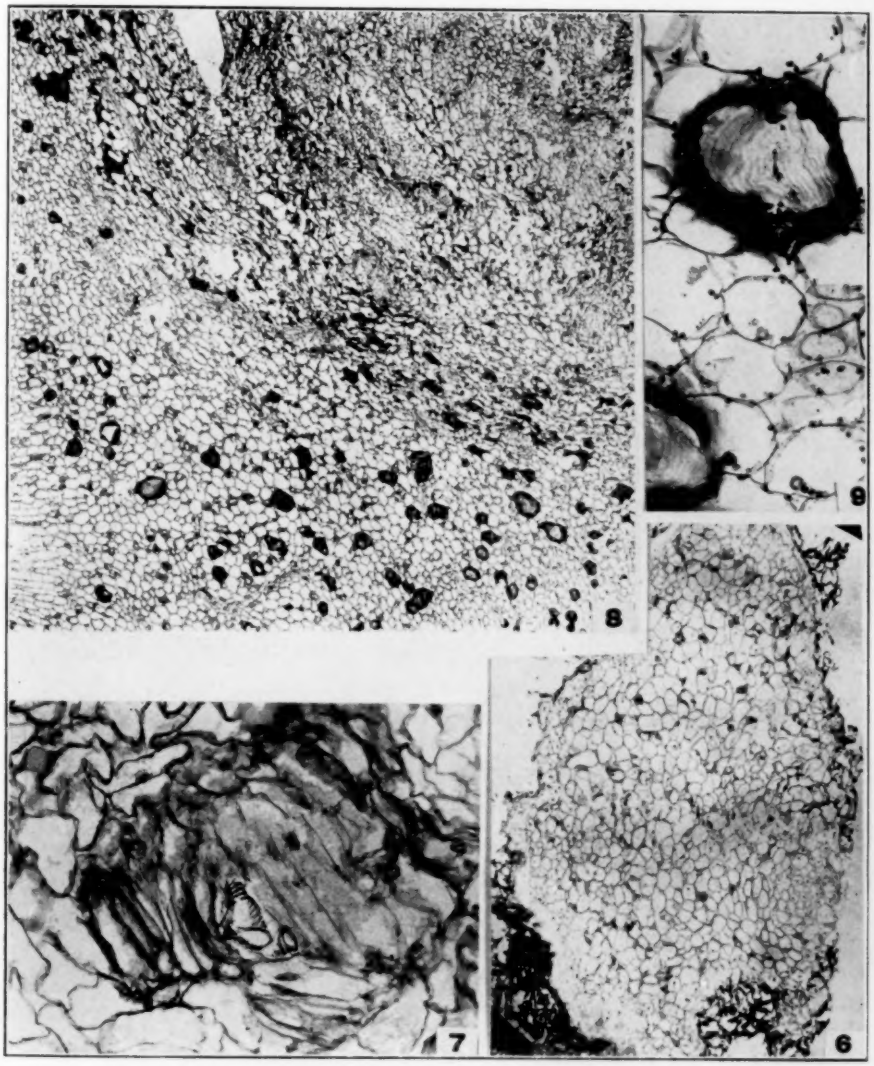

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Asterohyptis: a newly proposed genus of Mexico and Central America.

CARL EPLING

(WITH TEXT FIGURE)

Asterohyptis gen. nov.

Suffrutices ramosi ramulis gracilibus divaricato-ascendentibus; foliorum laminis nunc ovatis nunc lanceolatis sat magnis sat tenuibus, breviter petiolatis; floribus in cymulis densis in foliorum valde diminutorum axillis sessilibus, glomerulis globosis maximam partem spicas interruptas moniliformes formantibus rarius in spicas densas cylindratas congestis, bracteis lineari-setaceis brevibus subtentis; calycum florentium tubis campanulatis 10-venis, ore truncato nunc nudo nunc hirsuto, dentibus subulatis, nunc leniter recurvis nunc valde stellato-patentibus subaequilongis, in maturitate tubis paulo auctis cylindratis, dentibus fere immutatis; corollarum tubis cylindratis, superne leniter ampliatis intus hirtellis, laciniis subrotundis *subaequalibus lenissime bilabiatis*, labiae inferioris lacinia media leniter concava integra, in basi nullomodo angustata *nec in rugam contracta;* staminibus quatuor didymis, duobus posticis brevioribus saepius in tubo inclusis anticis e tubo breviter exsertis, omnibus *lenissime* declinatis; stylo breviter exserto ramis brevibus obovatis subplanis; gynobasis columella quam ovulis breviore; nuculis ovatis leniter complanatis minutissime punctato-rugosis.

Asterohyptis per *Hyptidem stellulatam, H. Mocinianam et H. Seemanni* constituta est; species typicam *A. stellulatam* designo.

Glomerula in maturitate 8–12 mm. diametro; calycum dentes 1.5–3.5 mm. longi.

Calycum florentium tubi 1.5–2 mm. longi, dentes maximam partem 1.5–2.5 mm. longi, in maturitate tubi 2.5–3.5 mm. longi; inflorescentia matura moniliforma ..... 1. *A. stellulata*

Calycum florentium tubi 1.2–1.5 mm. longi, dentes 2.5–3.5 mm. longi, in maturitate tubi 1.5–2 mm. longi; glomerula matura saepius in spicas cylindratas conferta ..... 2. *A. Mociniana*

Glomerula in maturitate 5–7 mm. diametro; calycum dentes .5–.7 mm. longi. ..... 3. *A. Seemanni*

1. A. stellulata comb. nov.

Hyptis stellulata Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr. 12:128.1848 per specim. in Mexico prov. Morelos prope Cuernavaca a Berlandier lectum constituta est; typum in herb. Kew., isotypos in herb. Mus. Brit., Berolin., Gray. et Vindob. vidi.

H. pubescens Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr.

12:128.1848 per specim. in Mexico a Moçino et Sesse lectum constituta est; typum verisimiliter verum e herb. Lambertiano in herb. Kew., isotypos probabiles in herb. Mus. Brit. vidi. *Mesosphaerum stellulatum* et *pubescens* Kuntze, Rev. Gen. **2**:526,527.1891 (nomina).

Suffrutex aromaticus altitudine 1–3 m. ramulis gracilibus divaricato-ascendentibus obtuse quadratis sulcatis, pilis brevibus nunc extensis nunc ascendentibus vestitis, internodiis 3–8 cm. longis; foliorum laminis maximam partem anguste ovatis, 3–8 cm. longis, 1.5–3.5 cm. latis, acutis, in basi nunc rotundato-truncatis nunc rotundato-angustatis, margine subdupliciter serrulata, crenis ad 1.5 mm. altis, pagina superiore viride hirtella, inferiore villosula etiam subtomentosa pallidiore etiam incana, petiolis ad 1.5 cm. longis

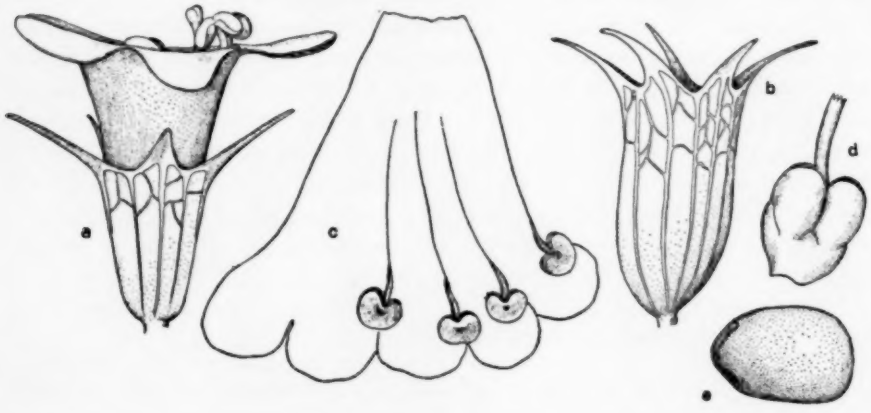

Fig. 1. *Asterohyptis stellata*. a, flower; b, mature calyx; c, corolla split open; d, ovules and gynobase; e, nutlet.

elatis; verticillastris in maturitate 8–12 mm. diametro, rarius in spicas cylindrates densas confertis; calycum florentium tubo *1.5–2 mm. longo*, dentibus *1.5 interdum 2.5 mm.* longis *saepius utrinque hirtellis*, in maturitate tubo *2.5–3.5 mm.* longo; corollarum tubo *1.5–2 mm.* longo; nuculis 1–1.2 mm. longis.

MEXICO: **Sonora:** in Sierra de los Alamos, 17.IV.1910, *Rose 12995;* **Sinaloa:** prope Balboa, I.1923, *Ortega 4985;* San Ignacio, 500 m., 9.III.1918, *Montes 265;* **Nayarit:** inter San Blas et Tepic, *Sinclair;* prope Acaponeta, 25. II.1927, *Jones 23154;* prope Acaponeta, 1.III.1927, *Jones 23152;* La Barranca, 21.II.1927, *Jones 23153;* prope Tepic, 9–10.II.1927, *Jones 23257, 23151;* prope Tepic, I–II.1892, *Palmer;* prope Ocotillo, 28.V.1849, *Gregg 958;* prope Tepic, II.1895, *Lamb. 523;* prope Acaponeta, 10.IV.1910, *Rose 14301;* **Durango:** Chocala, 5.III.1899, *Goldman 349;* **Zacatecas:** sine loco, *Hartweg 172;* **Aguas Calientes:** sine loco, *Hartweg 172;* **Jalisco:** sine loco, *Beechey;* Etzatlan, 5.X.1908, *Barnes et Land 242;* prope Guadalajara, 5000 ped., 6.X.1903, *Pringle 11677;* prope Guadalajara, 5000 ped., 9.X.1903, *Pringle 11676;* prope Tuxpan, II.1904, *Purpus 500;* in Cerro de Ameca, XII.1899, *Diguet;* in Barranca del Rio Santiago, X.1899, *Diguet;* prope Guadalajara, 22.X.

1889, *Pringle 2727;* ad Rio Blanco, 1886, *Palmer 326;* prope Magdalena, 24.V. 1849, *Gregg 882;* inter Huejilla et Mesquitec, 25.VIII.1897, *Rose 2563;* **Colima:** sine loco, 1891, *Palmer 1203;* **Michoacan:** Morelia, Loma Sta. Maria, 26.VIII. 1909, *Fr. Arsène 2971;* El Ocote, 500 m., 2.XI.1898, *Langlasse 690;* **Morelos:** prope Cuernavaca, 12–14.XI.1865, *Bourgeau 1277;* prope Cuernavaca, 20.X.1827, *Berlandier 1058* **T,** *959;* prope Cuernavaca, 31.VIII.1910, *Orcutt 3894;* prope Yautepec, 4000 ped., *Pringle 11100;* in collibus prope Cuernavaca, 5000 ped., 19.X.1900, *Pringle 9042;* in valle Toluca, X.1827, *Berlandier 1136;* prope Xochicalo ad Cuernavaca, XII.1887, *Seler 389;* San Anton prope Cuernavaca, 14.X. 1904, *Seler 4197;* in valle Toluca, X.1827, *Berlandier 1136;* **Oaxaca:** Oaxaca, 20.XI. 1895, *Seler 1358;* prope Oaxaca, XI.1840, *Galeotti 7137;* in valle Oaxaca, 5000 ped., 30.X.1894, *L. C. Smith 412;* prope Oaxaca, 5100–5800 ped., 8.IX.1894, *Nelson 1215;* Sierra San Felipe, 6000 ped., 11.VI.1894, *Pringle 5870;* in Sierra San Felipe, 7.IX.1921, *Conzatti 4212;* in Sierra de la Soledad, 20.XI.1895, *Seler 1358;* La Bastolo Youhtepec, 7.I.1896, *Seler 1658;* **Puebla:** Caxcotlan, 7000–8000 ped., IX.1909, *Purpus 4162;* **Vera Cruz:** Orizaba, 1853, *Müller;* Borrego, Orizaba, 16.IX.1866, *Bourgeau 3046;* inter Vera Cruz et Orizaba, *Müller 598;* in collibus aridis prope Orizaba, 29.IX.1923, *Smyth 164;* Orizaba, 4000 ped., 25–31.VII.1891, *Seaton 144, 35.*

2. A. Mociniana comb. nov.

Hyptis Mociniana Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr. **12**:128.1848 per specim. in Mexico a Moçino et Sesse lectum constituta est; typum verisimiliter verum e herb. Lambertiano in herb. Kew. vidi.

H. spinulosa Benth., Lab. Gen. et Sp. 129.1833 et in DC. Prodr. **12**:128.1848 per specim. in Mexico a Moçino et Sesse lectum constituta est; typum olim in herb. Lambert. hodie in herb. horti bot. Oxon. vidi.

H. stellulata var. *Sinclairi* Benth. in DC. Prodr. **12**:128.1848 per specim. in Mexico prope Acapulco a Sinclair lectum constituta est; typum in herb. Kew. vidi.

Mesosphaerum mocinianum Kuntze, Rev. Gen. **2**:526.1891 (nomen).

H. alopecuroides Briq. in Ann. Conserv. Geneve **2**:201.1898 per specim. in Costa Rica prope San Mateo a Biolley (in Pittier et Durand no. 7099) lectum constituta est; typum in herb. Delessert., isotypum in herb. Mus. Brux. et Smithson. vidi.

H. Biolleyi Briq. in Ann. Conserv. Geneve **2**:200.1898 per specim. in Costa Rica inter San Mateo et S. Ramon a Biolley (in Pittier et Durand no. 7010) lectum constituta est; typum in herb. Delessert., isotypum in herb. Mus. Brux. vidi.

Mesosphaerum alopecuroides Briq., loc. cit. (nomen).

M. Biolleyi Briq., loc. cit. (nomen).

Suffrutex altitudine 1–3 m. ramulis gracilibus divaricato-ascendentibus obtuse quadratis sulcatis, pilis brevibus extensis sparse vestitis, internodiis 3–8 cm. longis; foliorum laminis sat tenuibus anguste ovatis, 3–8 cm. longis,

1.5–3.5 cm. latis, acutis vel leniter acuminatis, in basi saepius rotundato-truncatus vel rotundatis, margine subdupliciter serrulata, crenis ad 1 mm. altis, pagina superiore hirtella, inferiore villosula vix tomentosa pallidiore vix tamen incana, petiolis 3–12 mm. longis elatis; verticillastris in maturitate 8–12 mm. diametro, *maximam partem in spicas cylindratas densas confertis;* calycum florentium tubo *1.2–1.5 mm.* longo, dentibus *2.5–3.5 mm.* longis, saepius anguste marginatis et *ad margines* solummodo hirtellis, in maturitate tubo *1.5–2 mm.* longo; corollarum tubo *2.8–3 mm.* longo; nuculis circa 1 mm. longis.

MEXICO: **Guerrero:** prope Acapulco, *Palmer 128;* prope Acapulco, *Sinclair;* prope Acapulco, *Barclay.* **Vera Cruz:** sine loco, *Mocino et Sesse* **T;** in valle Cordoba, 14.I.1866, *Bourgeau 1707;* prope Zacuapan in Barranca de Santa Maria in agris, XII.1906, *Purpus 2285;* prope Atoyac, XII.1882, *Kerber 170;* prope La Purga, 27.I.1906, *Greenman 223;* Orizaba, *Botteri 647;* **Chiapas:** prope Teopisco, 30.XII. 1906, *Collins et Doyle 121;* prope San Sebastian, 14.I.1907, *Collins et Doyle 189.*

GUATEMALA: prope Jumaytepeque, Santa Rosa, *Heyde et Lux 4109;* prope Gualan, 420 ped., *Deam 365, 366;* prope Agua Caliente, 10.II.1917, *Holway 848;*

HONDURAS: in silvis montanis ad Copan, 8.I.1897, *Seler 3330;* prope Ampola, Isla Tigre, 14.II.1922, *Standley 20714.*

SAN SALVADOR: in monte ignivomo San Salvador 9.I.1898, 7000 ped., *Niederlein 261;* sine loco, XII.1905, *Velasco 8872;* sine loco, *Calderon 2281;* prope Ahuachapan, 1923, *Padilla 509;* prope Ateos, 17.IV.1922, *Standley 23413;* inter San Martin et Laguna de Ilopango, 1.IV.1922, *Standley 22616;* prope San Vicente, 2–11.III.1922, *Standley 21222;* prope Ahuachapan 800–1000 m., 9–27.I.1922, *Standley 19945;* prope San Salvador, 650–850 m., 20.XII.1921–4.I.1922, *Standley 19153.*

NICARAGUA: prope La Paz ad vias, 31.I. 1903, *Baker210, 663;* Matagolpa, 500 m., 27.II.1894, *Rothshuh 507;* prope Grenada, XII.1869, *Levy 296.*

COSTA RICA: prope Nicoya, 1.1900, *Tonduz 13656;* prope San Mateo, *Pittier et Durand 7099;* prope San Mateo, 200 m., 20.I.1892, *Biolley 7103;* San Mateo et San Ramon, 400 m., 25.I.1892, *Biolley 7010.*

3. A. Seemanni comb. nov.

H. Seemanni Gray in Proc. Amer. Acad. **21**:407.1886 per specim. in Mexico occ. in Cerro de Pinal a Seemann (n. 1500) lectum constituta est; typum in herb. Gray., isotypos in herb. Kew. et Mus. Brit. vidi.

H. Seemanni var. stenophylla B. L. Robins. in Proc. Boston Soc. Nat. Hist. **31**:267.1904 per specim. in Mexico prov. Sonora prope Badehuache a Lloyd (no. 450) lectum constituta est; typum in herb. Gray. vidi.

Frutex habitus Buddleiae ramulis gracilibus subteretibus dense hispidulo-villosulis, internodiis 2–5 cm. longis; foliorum mediorum laminis oblongo-lanceolatis, maximam partem 5–8 cm. longis, 1–2 cm. latis, acutis, in basi rotundatis interdum angustatis, margine serrulata, crenis .5 mm. altis, pagina superiore hirsuta, inferiore villosa pallidiore interdum subglabra, petiolis 5–10 mm. longis elatis; floribus in paniculis *gracilibus moniliformis* subnudis, glomerulis compactis subglobosis incanis inter se 10 . . . 8 . . . 5 . . . 3 mm. distanti-

bus, *maturis 5–7 mm.* diametro; calycibus florentibus 1.5 mm. longis extus villosis, ore valde hirsuto, dentibus circa *.4 mm.* longis, in maturitate tubo paulo aucto; corollarum tubo 2 mm. longo; nuculis 1 mm. longis.

MEXICO: Rio de Aros, 7000 ped., *Townsend et Barber 400;* **Chihuahua:** in quercetis inter Reforma et Agua Caliente de Huachara, 25.XII.1904, *Endlich 750;* Batopilas, 5500–6500 ped., 4–5.X.1898, *Goldman 198;* sine loco, *Palmer 177;* Cerro de Pinal, XII.1848, *Seemann 1500* **T; Sonora:** Badehuache, 2.XII.1890, *Lloyd 450;* prope Alamos, 1890, *Palmer 398;* **Sinaloa:** Batel, *Dehesa 1624;* Villa Union, I.1922, *Ortega 4441;* Balboa, I. 1923, *Ortega 5050;*

Index Nominum.

Asterohyptis Mociniana Epl.
Asterohyptis Seemanni Epl.
Asterohyptis stellulata Epl.
Hyptis alopecuroides Briq.
Hyptis Biolleyi Briq.
Hyptis mociniana Benth.
Hyptis pubescens Benth.
Hyptis Seemanni Gray
Hyptis Seemanni var. stenophylla Robins.
Hyptis spinulosa Benth.
Hyptis stellulata Benth.
Hyptis stellulata var. Sinclairi Benth.
Mesosphaerum alopecuroides Briq.
Mesosphaerum Biolleyi Briq.
Mesosphaerum mocinianum Kuntze
Mesosphaerum pubescens Kuntze
Mesosphaerum stellulatum Kuntze.

Reproduction in the rusts

MABEL A. RICE

(WITH PLATES 4–6)

We have apparently reached a period of rapid advance in our knowledge of sexual reproduction in the rusts. The results gained from cultural methods, applied so successfully by Craigie (1927) under the leadership of Buller have quite re-established the tentative views of Meyen, Tulasne, and de Bary as to the nature and functions of spermogonia and spermatia though Craigie, Buller, R. Allen and Andrus make no reference to this earlier work.

Meyen (1841) writes: "Eine genauere Untersuchung dieser eigenthümlichen Bildung, welche den Aecidien-Pusteln stets vorangeht, so wie die Berücksichtigung der räumlichen und zeitlichen Verhältnisse, unter welchen jene beiden Bildungen zu einander stehen, veranlassen mich zu der Meinung, dass wir hier verschiedene Geschlechter eines und desselben Pilzes vor uns haben, dass nämlich das Aecidiolum exanthematum des Herrn Unger die männliche oder befruchtende Bildung der darauf folgenden wahren, sporen-artige Bläschen enthaltenden Aecidium-Pustel ist."

Tulasne (1854) states his agreement with de Bary, saying that "le premier (l'Aecidiolum) lui a semblé, comme à nous, offrir tant d'analogie avec les spermogonies des Lichens, qu'il ne fait pas difficulté de lui accorder le nom de ces organes et la même valeur physiologique, quelle qu'elle soit d'ailleurs. Cette valeur est effectivement incertaine, et le sera sans doubt longtemps encore."

De Bary (1887) writes:

"The spermogonia, where they occur, are always the precursors of the aecidia which belong to them, that is they are always present in a fully developed state when the first beginnings of the aecidia make their appearance in their neighborhood. All these facts point to a physiological relation of the two organs to one another similar to that which exists between the spermogonia and sporocarps of the Collemeae. But a more certain proof of this relation is still wanting; the organs in question must therefore for the present be classed with those in which the physiological import is doubtful."

Brefeld (1888) on the other hand disclaimed any sexual nature for the higher fungi and considered the spermatia of conidial nature. He writes: "Die Spermatien der Ascomyceten und namentlich der flechtenbildenden Formen unter diesen sind nur Conidien, . . ."

"Die Spermatien (of the Uredineae) in den kleinen Fruchtanlagen der Spermogonien sind die einfachen Conidien."

Arthur (1905), as a part of his new terminology for rust sori, substitutes pycnium for spermogonium and pycniospores for spermatia. In a later discussion of this terminology Arthur and Kern (1926) state: "It is proposed to use the term *pycnium* for the sori with inefficient spores. Neither the term nor the manner of defining it raises the question whether or not these are vestigial sex organs." Discussing the subject of sexuality among the rusts, Arthur (1929) supports this use of the term *pycnium*, writing: "Neverless, no process of sexuality embodying such a high type as just indicated (male and female organs) has yet been found in any species of the rusts although pycnia have from first to last maintained their reputation as male organs and correspond to such in details of gross and minute structure and in time and place of their appearance." He writes further, with reference to Craigie: "they (the pycniospores) may exert a quickening influence upon the development of the aecia."

Cunningham, (1932) however, discards the term *spermogonium* because of its sexual connotation. He states: "As this structure is not a male organ it cannot be termed a spermogonium." Like Arthur he objects to the term *pycnidium* on the ground that the rust structure is not homologous with the pycnidium of Ascomycetes. He modifies Arthur's term pycnium to pycniosorus but he adopts Arthur's term *pycniospore*.

Craigie (1927), following Arthur except for one difference in spelling, calls the receptacle a pycnium and the spores pycnospores which deBary called respectively spermogonium and spermatia. Craigie seems, however, to have made this choice because of the relation of these terms to pycnidium and pycnidiospores, terms commonly used for conidia borne in a flask-shaped receptacle, and seems to be following Brefeld and to be denying that these rust spores have any sexual character, at the same time that he is announcing the demonstration of their differentiation as plus and minus and their function in sexual reproduction. He writes: "The pycnospores are not functionless male gametes but are simply conidia corresponding to the uninucleate oidia which appear on the monosporous mycelia of such heterothallic Hymenomycetes as *Coprinus lagopus*, *Coprinus niveus*, *Stropharia semiglobata*, and *Collybia velutipes*." This might seem to imply the assumption of such sexually differentiated races as Dodge (1924) has found in *Caeoma nitens*, but in the absence of any statement from Craigie as to how such conidia germinate and the specific part they play in developing the aecidium the statement is rather confusing.

The historical survey of views concerning the function of the spermatia of the rusts made by Blackman and by Klebahn in 1904 and by

Moreau in 1913 continued to be adequate for the subject until the work of Craigie was published in 1927. They held respectively that the "spermatia are male cells which have now become functionless"; that "die Spermogonien als Organe anzusehen, denen gegenwärtig im Leben der Rostpilze keine Bedeutung mehr zukommt, . . . Man könnte auf den Gedanken kommen, dass die Ausscheidung eines Teils seiner Substanz für die Weiterentwickelung des Pilzes nützlich wäre"; "que nous nous trouvons en présence de deux opinions presque également soutenables: ou bien ce sont des spores asexuelles et alors elles ne jouent pratiquement aucun rôle, ou bien ce sont des vestiges de gamètes mâles et jusqu'ici aucune tentative pour retrouver les vestiges des gamètes femelles correspondants n'a donné pleine satisfaction. C'est la découverte d'organes sexuels femelles vestigiels qui seule, dans l'état actuel de nos connaissances, nous paraît capable de forcer l'opinion en faveur de la nature sexuelle des spermaties."

It becomes now more than a theoretical question to choose between the two terms, spermatia and pycniospores. In support of the former term excellent evidence for the morphological identity of spermatia and microconidia, which Tulasne (1861, 1931) distinguished by the criterion of non-germination or germination respectively, may be found, in the three groups Ascomycetes, ascomycetous lichens, and rusts, by a review of the different types which are present in each of these groups.

In the Ascomycetes the Sclerotinias of Woronin (1888) bud off what he called "spermatienähnlichen Sporidien" from all parts of the mycelium and from conidia and ascospores. *Sclerotinia Duriaeana* (Whetzel, 1929) produces microconidial sporodochia. Whetzel did not attempt the germination of the microconidia but states; "They more probably function as do the spermatia of the rusts (Craigie 1927)." *Neurospora sitophila* (Dodge, 1930) bears. on branches of the mycelia, microconidia which Dodge calls "clearly homologous with the microconidia of *Sclerotinia*"; *Sclerotinia Gladioli* (Drayton, 1932) bears microconidia in sporodochium-like masses; *Pleurage anserina* (Ames, 1932) bears microconidia on branches of the mycelium. Drayton (1932), Dodge (1932), and Ames (1932) have proved these microconidia to be functional male gametes.

An intermediate between this diffuse type of bearing male cells and the spermogonium and spermatia of the *Collema* and *Physma* studied by Stahl (1877) is illustrated in the form of *Collema pulposum* studied by Bachmann (1912). In this last case the reduction in number and mobility of the spermatia is correlated with the great length of the trichogyne which thus "seeks out" the spermatia. This sessile habit of the spermatia leads over to the single and sessile antheridia of *Ascobolus magnificus* and *Py-*

ronema, and to the still more reduced habit of *Sphaerotheca*, *Ascobolus furfuraceus*, *Gymnoascus*, etc.

The occurrence of spermatia in crusts on stromata is a different type. The occurrence of spermatia in such crusts under and following conidial crusts is figured by Higgins (1914) for *Coccomyces hiemalis* and is reported by Backus (1932) for the same fungus. In the rusts one finds such a caeomatous habit of bearing spermatia in *Peridermium cerebrum* and *Peridermium Strobi* (Arthur's (1929) subcortical type).

There is also found in each of the three groups: Ascomycetes, ascomycetous lichens, and rusts, the very different type of spermatial development in pycnidium-like receptacles. In the Ascomycetes pycnidium and spermogonium are linked by forms in which spermatia develop after the pycniospores in the base of the same pycnidium. This is figured by Longyear (1904) for *Guignardia Bidwellii*, by Stewart (1916) for *Guignardia aesculi*, by Klebahn (1918) for *Mycosphaerella maculiformis*, and by Higgins (1920) for *Sphaerella Bolleana*.

For spermatia borne in separate spermogonia, in the Ascomycetes Higgins (1914) figures *Mycosphaerella personata;* in the lichens Stahl (1877) figures the characteristic type for *Physma compactum*. This is in general the type so common among the rusts although there are characteristic differences. The well developed wall of the lichen spermogonium is lacking in the rusts and the paraphyses of the rust spermogonium are lacking in the lichens. With the subepidermal type of Arthur's classification as the normal, the flask shape of the rust spermogonium varies from the high, stalked spermogonium of *Caeoma nitens* to the other extreme of Arthur's subcuticular type where the flask shape is much flattened and paraphyses are few or lacking. In the greater development of paraphyses and in the abundance of a sweet sticky secretion the spermogonia of the rusts seem the more highly developed organs, adapted to terrestrial conditions and insect dissemination. Rathay (1883) established by observations upon twenty different rusts the facts that insects are attracted by a reduction sugar present in the fragrant exudate of the spermogonia and that spermatia are carried in the exudate. He made records of the species and the relative numbers of insect visitors and concluded "dass die Insecten zu den reifen Spermogonien der Rostpilze in einer sehr volkkommenen Weise gelockt werden."

In considering the sexual nature of spermatia and microconidia such confusion as Craigie's might be avoided by following Allen (1929) in recognizing the distinction between (1) characters which distinguish gametes, sex organs, or individuals as male or female and (2) characters which regulate syngamy. The latter are to be regarded as the primitive factors in sex-

ual reproduction since they include the capacities arising with sexual maturity. Cells fuse because they are mature, and have gained different powers with that maturity. Spermatia are produced because the mycelium which bears them is mature and they fuse with other cells because, as cells, they are sexually mature. That they differ structurally and functionally from egg cells is an adaptation to facilitate this fusion. As a familiar illustration,—cells of *Spirogyra* filaments develop in a more or less dense mass where they might readily fuse at any time but they continue their development by division only, until maturity. Maturity brings a change from the asexual habit to the habit or capacity for cell fusions. At sexual maturity conjugations may occur between cells in the same or in different *Spirogyra* filaments. From such fusions it is postulated that organisms may result which are better equipped for their environment and have a better chance for survival. The initiation of variation and its degree may be increased by cross-fusions (mixie). Possibly this advantage determines the perpetuation of the fusion of unlikes. At least it is obvious that many devices regulate syngamy in the interests of the less certain cross-fusions. Allen illustrates by dichogamy and heterostyly in the seed plants upon which may depend the possibilities of self-, close-, or cross-pollination and subsequent syngamy. He also places in this category the various compatibilities which result in group intra-sterility and inter-fertility in such a species as *Nicotiana*. By holding to these distinctions, as Allen points out, the difficulties of thinking in terms of sex of several plus and minus races disappear. When *Schizophyllum commune* (Kniep, 1922), *Hypholoma fasciculare* (Funke, 1924), and *Coprinus lagopus* (Hanna, 1925) are reported to be four-sexed we should think, not of bipolar characters of maleness and femaleness, but of multipolar characters which, through group compatibility or incompatibility, further or inhibit syngamy. This distinction obviates Craigie's objection to the term spermatia for spores which show plus and minus characters. The property of maleness, a character of sexual differentiation, placed by Allen in his first category may coexist with degrees of compatibility, characters favoring or hindering syngamy, placed by Allen in his second category. Ruth Allen (1930) fails to draw this distinction when she writes of the spermatium: "Nor can it be considered a vestigial male organ, for, as Craigie has pointed out, half of the pycnia are of one sex and half of the other, although they look alike." In a later paper Ruth Allen (1932) writes: "The word 'spermogonium' implies a male structure. It should not be forgotten, however, that when nectar is interchanged between two infections of different sexes each fertilizes the other." Here evidently the term "male structure" refers to a first category character; likewise the term "fertilization," but the phrase,

"two infections of different sexes" refers, as she has explained earlier, to the plus and minus character of two monosporidial mycelia. These are, I think, characters of the second category.

We shall do well to use terms with the utmost care in a field so complicated as that of sexual reproduction in the fungi and algae. The distinctions which I have attempted by the use of Allen's categories raise other questions of terminology. Compatibility and incompatibility imply that mature germ cells which are functionally effective in a given combination may be quite non-functional in another. They do not imply the sex of Allen's first category. The genetic origin of these evolved differences in compatibility is more easily explained when they fall into two groups only and are, as Gwynne-Vaughan (1932) suggests, "complementary" but there are multipolar groups to be reckoned with and in these the compatibility relations will probably give the key to the solution. In the fungi perhaps the best known cases of multipolarity in compatibilities are among the Hymenomycetes where their origin in the basidium indicates a segregation of factors by reduction division.

Allen (1932) in a more recent discussion of the sex problem attempts to name and classify the genetic factors which have to do with sex as contrasted with the sex characters themselves. He recognizes three genetic classes. He describes maleness and femaleness as the effects of (1) *sex-potency factors* which are present as a pair of potentials in every organism. The exceptions to the resultant hermaphroditism he sees as the inhibiting effect of (2) *sex-tendency factors* located possibly in the X-Y chromosomes. The many other diverse genetic factors which influence sex expression, Allen groups under the term (3) *sex-influencing factors*. Allen's second discussion, by the illustrations of the workings of sex-potencies and sex-tendencies, clarifies our conceptions of heterothallism even though it is from the Angiosperms that he draws his most distinctive illustration. The heterothallism brought about by the inhibition of a sex-tendency factor upon the sex-potency factors which effect a homothallic condition is a structural heterothallism, a first category sex character. It becomes clear, by contrast, that the heterothallism under discussion in the fungi is one of incompatibility.

Allen notes the infrequency of the occurrence of structural heterothallism among the Angiosperms. His illustrations from the sporophytic stage of the Angiosperms would, according to Blakeslee (1906), be examples of heterophytism rather than heterothallism. Allen makes the distinction in pointing out that the gametophytic stage of the Angiosperms is always functionally unisexual. Too little is known yet about the Thallophytes in relation to sex classes to generalize but it is possibly significant that several

recent reports announce determinations of self sterility in connection with homothallism. Rosenvinge (1929) has reversed Darbishire's (1899) statement that *Phyllophora Brodiaei* is dioecious. He finds both sex organs present on each plant although they do not function. Drayton (1932) writes of *Sclerotinia Gladioli*, "It was also demonstrated that the receptive bodies of each isolate do not react with their own microconidia; that is, they are all self-sterile." Ames (1932) reports *Pleurage anserina* to be hermaphroditic but self-sterile. Gwynne-Vaughan (1932) reports two strains of *Ascobolus magnificus* in which all thalli are capable of bearing both male and female organs but in which fruit can only be formed when two "complementary" mycelia are intermingled.

Gwynne-Vaughan does not admit this difference in complement in the strains of *Ascobolus magnificus* as a distinction of sex. Although she does not give a name to the character, her illustration of self sterility in *Primula* suggests incompatibility. She sees the character in *Ascobolus magnificus* operating through the male and female organs, and, in such fungi as lack the male or female organs or both, she sees it acting as a substitute character which gives physiologically the same effects as sexual union. It seems to me that Allen's system of two sex categories, as outlined above, is preferable as a system by which to distinguish the quite different characters which we are coming to realize are confused under the convenient terminology introduced by Blakeslee (1906).

In his work with *Neurospora* Dodge (1932) has called those races heterothallic that will produce perithecia only when two different strains are brought together. Dodge reports that this mating of strains may be between mycelia obtained either from ascospores, from macroconidia, or from microconidia which he has germinated in often-repeated experiments. Each mycelium, however, Dodge points out produces microspores or macrospores in addition to ascogonial coils and the primordia of perithecia. He finds that either macroconidia or microconidia may function in initiating perithecial development. Upon the basis of these data Dodge, one would think, by his reference to the Kniep-Correns theory, draws the same distinctions that Allen has made for the Angiosperms with reference to sex-potency and sex-tendency factors. He writes, "Kniep points out that one could assume with Correns in accounting for the reactions of our so-called heterothallic Ascomycetes that each haploid mycelium contains potentialities of both male and female sexes, but that there are genes, determinators, that impress on such a mycelium either a male or a female stamp when it comes to the origin of fruit bodies." Dodge states that any monosporous mycelium of *Neurospora* "is, to all intents and purposes, unisexual when it comes to sexual reproduction." This must be, however,

because of self-sterility rather than the segregation of sexes. Turning to *Pyronema* where both of the sex organs are known, he sums up: "The development of antheridial branches as distinct from oogonial branches in *Pyronema* is a case of sex differentiation and not sex segregation. It is a coming to maturity of the mycelium."

It seems clear that Craigie is wrong in likening the "pycnospores" to the sporidia of the Hymenomycetes. It is today a generally accepted fact that the teleutospore with reduction division in the promycelium is homologous with the basidium of the Hymenomycetes. The homology may be extended to include the Ascomycetes. Harper (1905) writes: "If the evidence advanced by Mottier and Williams that a reduction division occurs in the development of the tetrasporange be confirmed, it is plain that the homologue of the ascus and the teleutospore, and of the basidium as well, is in the tetrasporange and not in the carpospore, as many have been inclined to assume." The spermatia, Craigie's "pycnospores," are haploid spores, developed upon a mycelium, the outgrowth of a haploid sporidium. It is not strange then, that with such a derivation there should be compatibility or incompatibility in the reactions of the gametophytic mycelia. This heterothallism belongs in Allen's second category: it is a functional rather than a morphological dioecism.

The discovery that there are degrees of compatibility in the rusts is a distinct contribution but this discovery merely brings the rusts into line with the other great groups of plants in which an increasing mass of evidence leads us now to expect to find that syngamy is regulated in the interests of cross-fusion. The crux of Craigie's work is his evidence that the spermatia, which have long been thought functionless, are in reality a necessary link in the production of aecidiospores. Craigie seems only concerned with heterothallism when he lists "three ways in which pustules of monosporidial origin may change from the haploid to the diploid condition" and he confines himself to the mention of fusions between plus and minus mycelia or plus and minus "pycnospores." Ruth Allen recognizes the two distinct problems. Yet curiously enough her reports of attempts to find out by cytological methods, the details of fertilization she entitles merely, "Heterothallism in *Puccinia graminis*" (1930), and, "A cytological study of heterothallism in *Puccinia triticina*" (1932).

REVIEW OF LITERATURE

Comparatively little cytological work upon reproduction in the rusts has been published since Craigie's discovery. Hanna (1925) found that aecidia of *Puccinia graminis* in monosporidial infections were composed of a haploid mycelium and were sterile, while infections in which spermo-

gonial nectar had been mixed produced aecidiospores from a diploid mycelium.

Andrus (1931) found evidence of heterothallism in *Uromyces appendiculatus* and *Uromyces Vignae* and also made a cytological examination of the spermogonial and aecidial development of these rusts. He emphasizes the latter by his title: Sex in *Uromyces appendiculatus* and *Uromyces Vignae*. Andrus regards the spermatia as functional male gametes. He interprets as trichogynes the hyphae which he finds projecting through stomata or between epidermal cells. In a few of these he observes a binucleate condition. He has not been able to trace this "trichogenous hypha" to the egg cell which he locates at the base of each spore chain in the aecidium but he interprets the "two-legged" cells which he finds there as egg cells each with a trichogenous branch and a foot-cell. He figures the passage of what he believes the nucleus of the spermatium from this trichogenous branch up into the egg-cell. These "ruptured hyphae" and their binucleate condition may, I think, be open to another interpretation since the bean rust is an autoecious rust. It is a question as to whether the hyphae which Andrus saw at the surface of the leaves are not infection hyphae from aecidiospores. An intermingling gametophytic and sporophytic mycelium has frequently been reported for rusts of this class. Sappin-Trouffy (1896) mentions such a condition for *Puccinia Violae;* Fromme (1914) for both *Puccinia Violae* and *Puccinia Claytoniata*. Olive (1908) reports intermingling mycelia for *Puccinia Podophylli*.

Ruth Allen (1930, 1932) has published two papers which give cytological details of stages in the reproduction of *Puccinia graminis* and *Puccinia triticina*. Her data upon the two critical points in the reproduction process (the function of spermatia, and the initiation of the spore chains in the aecidium) effect an alteration in her theories as given in the first and the second papers. Binucleate cells found in the region of spermogonia in the mycelium of *Puccinia graminis* lead her to place the initiation of the sporophytic generation there but she emphasizes the view of Cragie that the spores which function there, either directly or indirectly, are non-male, plus and minus pycniospores. In the mycelium of *Puccinia triticina*, however, she finds hyphae which penetrate the stomata of the host from below and end at once in enlarged finger-like tips. In the substomatal spaces she finds binucleate and multinucleate cells. Allen does not report seeing fertilization but the nuclear conditions described in the substomatal hyphae, taken in conjunction with Craigie's evidence that spermatia play a part in the development of aecidiospores, she regards as indirect evidence that these protruding hyphae are "receptive hyphae." She returns, therefore, to the idea of the earlier mycologists that spermatia are functioning

male gametes, instead of pycniospores. Allen does not refer to the fact that similar protruding hyphae were earlier reported, although lacking evidence of fertilization they were not regarded as trichogynes. I am not sure whether de Bary (1887) was the first to observe them, but his description fits Allen's figures. "In young groups of aecidia a phenomenon is observed not infrequently and without great difficulty, which seems to be in favor of the supposition that there is an archicarp duly equipped for conception; short obtuse hyphal branches project from some of the stomata like the tips of the trichogyne in *Polystigma* and may be traced here and there to a young perithecium." Klebahn (1904) has also described the same structures. "Man findet vielfach Hyphenknäuel, die sich unter den Spaltöffnungen angesiedelt haben, und durch den Spalt selbst ein kleines Hyphenbündel nach aussen schicken; am äusseren Rande des Spaltes endigen die Hyphen gewöhnlich mit einer kleinen Anschwellung. Gar nicht selten werden auch Spermatien bemerkt, welche an diesen Hyphen zu sitzen scheinen. Dies ist aber nichts auffälliges, denn die Spermatien finden sich in Menge auf der Epidermis und dürften sich also besonders leicht im Schutz der Erhöhungen und Vertiefungen der Spaltöffnungans ammeln."

In discussing the second critical point (the initiation of the spore chains in the aecidium) Ruth Allen emphasizes again the significance of the multinucleate cell. In *Puccinia graminis* she finds this first in the anlage of the aecidium and interprets it as the result of nuclear division in the sporophytic mycelium. In *Puccinia triticina* she finds the multinucleate condition also in hyphae of the sub-stomatal chamber and she interprets this as due to the entrance of many spermatial nuclei into one "receptive hypha." It is true that a "receptive hypha" functioning as a trichogyne may receive several male nuclei. Wolfe (1904) figures this for *Nemalion*. The hypha may merely transmit these spermatial nuclei to distant egg cells but here again we have precedent for considering the trichogyne as the accessory of a single egg cell while Allen seems to think that these same nuclei (the many male nuclei and the "native nucleus" of a hyphal cell) are present in the multinucleate cells of the aecidium from which she reports that the spore chains bud off. The actual contacts of spermatia with the trichogyne were not seen and the supposition that the multinucleate condition is the result of nuclear divisions, as Allen first suggested, would seem to be at least as likely, as that of the entrance of many spermatia. This supposition that the nuclei of many spermatia are present in the multinucleate cell of the aecidium makes more difficult any explanation for the condition reported by Allen (1930) for *Puccinia coronata* where she reports the finding of multinucleate cells, often of monstrous size, "in practically 100% of all the older sterile aecia."

Multinucleate cells in the base of an aecidial primordium have been frequently reported. Allen, in her paper upon *Puccinia graminis* lists nine workers since and including Blackman who report the phenomenon. The majority of these report cases of tri- and quadri-nucleate cells which give rise to chains of spores of the same nuclear number. Fromme (1912) in addition to this figures one case for *Melampsora lini* of a spore-mother cell with eleven nuclei. He interprets all the cases as due to the fusion of more than two cells for the formation of the "basal cells." Colley (1918) reports multiple fusions in aecidia of *Cronartium ribicola* and finds the number of polynucleate spores relatively so small that he concludes "either the extra nuclei so common in the basal cells degenerate or the complex basal cell gives off more than one binucleate spore chain." He finds some evidence in *Cronartium ribicola* that aecidiospore chains arise by branching from a large basal cell as Dittschlag (1910) and Hoffman (1912) figure for *Puccinia falcariae* and *Endophyllum Sempervivi*, respectively, Olive (1908) alone reports multinucleate cells in the aecidium as a possible normal condition for rusts in general. "That multinucleated cells are formed probably as regular occurrences during the earlier stages in the development of the young aecidia is indicated by their discovery during the course of this investigation in at least eight or ten species of rusts. I am therefore convinced that they are perfectly normal occurrences, and that they result simply from the nuclear divisions going on much faster and thus getting ahead of cell divisions." It is to be noted that Olive places the occurrence of the multinucleate cells after the cell fusions at the base of the spore chains. "While the part which these multinucleated cells take in the development of the aecidium is as yet somewhat obscure, the evidence appears to point to the conclusion that they are sporophytic structures and that they result from the stimulated growth which follows the sexual cell fusions."

Allen finds no cell fusion of the characteristic Christman type. In the earlier paper she treats the many cases heretofore reported of this type of fusion as possible instances of homothallism in the rusts. In her later paper she is inclined to question the occurrence of such fusions as the initiation of spore chains. "It is evident that the presence of a 2-legged basal cell is not in itself proof of fusion. In the past the presence of a few 2-legged cells in the layer of basal cells has sometimes been the only evidence offered that the sporophyte originated by fusion of pairs of uninucleate cells in the sporogenous area in the aecium. Without a study of younger stages, there is a risk of error in this assumption."

Fusions as the initiation of basal cells are the only type which are discussed by Allen. It seems to me that fusions might be considered in con-

nection with the development of the multinucleate cells in the aecidium. Allen does not report seeing any such fusions but the irregular lobes figured in her Plate 11, A-G suggest the possibility. This is one of the considerations which "the background of a red alga ancestry" (Dodge 1929) would suggest and Allen (1932) now considers the "probability of phylogenetic relationship between the two groups."

INVESTIGATIONS

Materials and methods

I have made a cytological study of spermogonial and aecidial stages of *Puccinia Sorghi* and also, to a lesser degree, of *Aecidium punctatum*, *Puccinia Violae*, and *Uromyces Caladii*. The three latter were all studied from field collections of the infected hosts: *Hepatica acutiloba*, *Viola cucullata*, and *Arisaema triphyllum*, respectively. For the study of *Puccinia Sorghi* teleutospores were supplied by E. B. Mains; Oxalis plants were collected from greenhouses at the New York Botanical Garden, Columbia University, and Wheaton College as it was too early for Oxalis in the field when the work was started. These plants were of two species: the familiar garden weed, *Xanthoxalis stricta* (L.) Small, and a small red-leaved form abundant as a weed in the plant house at Columbia University which, according to Bailey, is the tropical *Oxalis repens*, Thumb. a variety of *Oxalis corniculata*, Linn. (*O. stricta* L.), *Xanthoxalis corniculata* (L.) Small. Both varieties proved susceptible to the rust but the larger leaves of *Xanthoxalis stricta* were used for the cytological work. Inoculations were made both by moistening leaves with water into which teleutospores had been scraped, and by suspending the rusted corn leaves above the Oxalis plants by pressing the leaves into dishes of mud and inverting these over glass cylinders, after the method described by Allen. Both methods gave abundant infections. Monosporidial inoculations were not made.

Samples of leaves from inoculated plants were fixed at two-day intervals from two days after inoculation until after the discharge of aecidiospores. In the delicate leaves of Oxalis Flemming's medium solution caused shrinking of the hyphae. Fixations were made in Flemming's weak solution, Allen's B-15, Carnoy and 50% alcohol. Flemming's weak solution and Allen's B-15 proved the most satisfactory fixatives. For the fixation of *Puccinia Violae*, *Uromyces Caladii*, and *Aecidium punctatum* Flemming's medium solution was used. Sections were cut 5μ or 7.5μ thick and were stained with the triple stain.

OBSERVATIONS

Puccinia Sorghi. The first visible signs of infection on the Oxalis are yellow flecks which appear in from five to seven days after inoculation. They develop on the blades of the leaves but not on the petioles. From the inoculations described above the infections were merely sporadic. It was therefore difficult to detect the earliest signs of infection among the many healthy leaves. Spermogonia appeared in eight or nine days as tiny orange pimples in close clusters on both surfaces of the leaves. They are, however, more abundant on the upper leaf surface. They exude nectar abundantly for several days. Aecidia develop outside the clusters of spermogonia, forming, in the case of isolated spermogonial clusters, a complete circle around the cluster. They are erumpent in about two weeks after inoculation. The peridium is shaped like a slender jar with a slightly constricted mouth and is about three times the thickness of the leaf in height. The infected area is yellowed and is hypertrophied to twice the normal thickness of the leaf, chiefly by the elongation of the palisade parenchyma. The infected leaves age rapidly. By the time the aecidia of an infected leaf were all erumpent the leaf was generally withered and the plant with its indeterminate growth appeared quite healthy.

Aecidium punctatum. The stages of *Aecidium punctatum* were obtained from a single Hepatica plant which has been under observation for several years in a wood garden at Wheaton College. During this time rust has developed regularly on this one plant while none of the other Hepaticas in the garden plot have shown any rust. The rusted plant is sterile; the first leaves appear while the other plants are sending up blossoms. The folded leaves, when they first appear above ground, are punctate with spermogonia. Instead of growing in close-set clusters as do those of *Puccinia Sorghi*, single spermogonia dot thickly both surfaces of the leaves over all but the basal part of the blade. The brown hemispherical pustules glisten with an exudate when ripe and later persist as dry brown pimples. Aecidia develop within the same areas but open more frequently on the lower surface. The white peridium torn into four or more irregular lobes around the brown spores gives, at close view, a flower-like appearance to the aecidium. A second contrast to *Puccinia Sorghi* may be noted in the leaves of the Hepatica host. Instead of the localized changes described for Oxalis there is hypoplasia of the blade and hypertrophy of the petiole. The leaf is not yellowed but the blade is less divided than normal and stands erect on an abnormally long petiole as has been well figured by Arthur (1929). The rusted leaves do not live over winter after the habit of healthy Hepatica leaves. After four or five rusted leaves have appeared these are

followed by a whorl of healthy leaves. In June the green rusted leaves with their dried pustules stand erect in the center of a spreading circle of healthy leaves. In the fall there is no trace of the rusted leaves and sections of the persisting leaves do not show a mycelium.

Uromyces Caladii. Rust develops on *Arisaema triphyllum* with the unfolding shoot. The pale yellow spermogonia dot the surface of stem, petiole, leaf blades, spathe, and spadix. Aecidia are most abundant on the leaf tissues. The gray-white aecidia are much shallower cups than either *Puccinia Sorghi* or *Aecidium punctatum.* The material used for examination was erumpent with both spermogonia and aecidia.

Puccinia Violae. No succession of stages was examined in the violet rust. The violet plants were found heavily infected at the time of their blooming. Both spermogonia and aecidia were erumpent on thickened galls which were abundant on petioles and veins of the leaves.

Under microscopic examination I found in the rusted violet tissue binucleate hyphae which seemed somewhat like those described by Andrus for the bean rust as trichogynous hyphae (figs. 16, 17) but in reality, in my opinion, these hyphae extend through the stoma and are infecting hyphae from aecidiospores. Since the violet leaves at the time of fixation showed an abundance of ripe aecidia there must have been full opportunity for a reinfection by aecidiospores. Binucleate hyphae could be traced from stomatal regions into the weft of hyphae which separates the very loosely built parenchyma from the lower epidermis. This is the region where aecidia develop. There may be some connection here but I have already called attention to the fact that the occurrence of binucleate hyphae intermingled with the uninucleate stage of the violet rust has been reported by Sappin-Trouffy (1896) and Fromme (1914) who consider that they are sporophytic hyphae developing from germinating aecidiospores. I have already called attention to the question of interpretation which this fact raises for the autoecious bean rust. It is true there may be other hyphae in these tissues which are protruded from stomata or between epidermal cells instead of being in process of entering as infection hyphae. I found in the violet leaf an occasional stoma plugged by a fragment of a dead, red-staining hypha much like those which I have found in Oxalis. (fig. 18). Earlier stages would, however, be needed before one could with certainty distinguish two types of stomatal hyphae in the violet rust.

I examined only a small amount of the rusted *Arisaema* tissue but here also red-staining hyphal plugs were frequently found in the stomata (fig. 20). Here also the autoecious character of *Uromyces Caladii* makes the interpretation of any binucleate condition indeterminate.

In *Puccinia Sorghi* I have not yet found the stages showing infection of the Oxalis leaf by the sporidia of the rust but the infection hyphae in epidermal cells of the Oxalis leaf are abundant and conspicuous. Figure 1 shows one which was still alive in a leaf which was dotted with spermogonia and young aecidia fifteen days after inoculation. The original hypha is usually heavily sheathed and can be recognized long after the cell content is gone. In addition to sending branches into the intercellular spaces below they usually make a vigorous growth in the epidermal cell in the vicinity of the host nucleus. Such a tangled mass as is shown in the figure would presumably send out many hyphal branches. The cell figured lies close to a spermogonium on the left and the hyphae in the intercellular space on the left form part of the spermogonial tissue. By their perforation of an epidermal cell wall instead of entrance through a stoma, by their heavy sheath and persistent penetration beak they are readily distinguished from certain finger-shaped hyphae which I have found protruding from stomata of the Oxalis leaf.

Branches from the infection hyphae penetrate between the palisade cells and also form horizontal runners between the epidermis and the palisade. Long runners also follow the veins while the very slightly developed spongy parenchyma is crowded with a network of hyphae.

Haustoria are sent abundantly into the host cells from the intercellular hyphae. They are branched, much coiled structures arising from a short, slender entrance stalk. They have frequently more than one nucleus. They are in the great majority of cases coiled around the host cell nucleus. Invagination of the host cytoplasm is evident. Encasement or sheathing of the haustorium is rare but I have made no attempt to trace developmental stages of the haustorium in Oxalis.

From hyphal runners under the epidermis, particularly under the upper epidermis, short hyphae push out through the stomata. Sometimes as many as eight project through a single stoma. This can be seen best in a tangential section of a stoma but in a cross section view of a stoma the single hypha often proves, by a study of successive sections, to be one of a group. In figure 12, e, a fourth hypha is visible at an upper plane. These may usually be traced to separate origins from a runner or from several runners which crowd against the epidermis; less frequently they arise as a tuft from one branch. The cross section of the runner at the base of a hypha is a distinctive character in views of a single detached hypha. On account of the abrupt change of direction which these hyphae make in passing through the stomata this detached stomatal plug is the view most frequently seen of the branches. The central hypha in figure 4 shows the cell from the runner; also figure 18 from violet rust. The selection of views

on the plates is misleading in that this most characteristic view has been passed over and the occasional cases chosen which show more of the mycelium. These hyphae project from both the upper and the under surfaces of the leaf in the vicinity of spermogonia and aecidia. I have seen them just outside the paraphyses in surface views of epidermis which I have stripped from a leaf and mounted in lactophenol. Sections of the leaf prove that they are an almost constant accompaniment of the spermogonium. They are crowded so close to it that they seem to come from the ostiole but they are in reality outside the paraphyses. Figure 13 is taken from an outer vertical section of a spermogonium and shows the striking contrast between these short, blunt, red-stained tips and the long slender, pointed paraphyses. Figure 2 shows a stoma which lay just to one side of a spermogonium. The attachment of the projecting hyphae can be traced to the pseudoparenchyma of the spermogonium. Should these hyphae prove to be trichogynes there might prove to be significance in Fromme's finding spermogonia borne in the center of aecidia in *Puccinia Claytoniata*. "The condition," he writes, "is evidently abnormal, but could have been construed as proof of a sexual relation between the spermogonium and aecidium by the older exponents of this view." Even more suggestive is Stahl's (1877) figure for *Physma compactum* of a vertical section of a spermogonium with trichogynes arising from the basal pseudoparenchyma and reaching the surface on both sides of the ostiole.

These hyphae also project from stomata in the vicinity of aecidia. Figure 5 shows one in front of a guard cell of the lower epidermis. It can be traced into the pseudoparenchyma below a young aecidium. The abrupt turn is characteristic of hyphae in this position. They seem to become part of the enclosing plechtenchyma of an aecidium. Possibly it is by this indirect approach that they reach the basal anlage of the aecidium. Figure 6 and the enlargements shown in figure 12, a–d, f, are drawn from a section containing two aecidia which have well developed spore chains but which have not broken the enclosing tissue. In one of the microscopic fields five groups of hyphae project from stomata on the under surface. These lie two to the left and three between the two aecidia. Blue-stained hyphae can be traced from these regions through the yellow-stained mass of hyphae which fills the substomatal regions and by the same difference in color they can be traced interruptedly into the plectenchyma of the aecidia. Bachmann (1912) has noted the same differential staining for the trichogynes of *Collema pulposum* in the lichen stroma. The above mentioned section was made from a leaf portion on which half-grown aecidia surrounded a group of old spermogonia. As one looks over the sections of this material one is impressed by the abundance of the hyphal tufts which

project from stomata. They occur near the spermogonia in positions which I have described above but they occur more abundantly on the under epidermis near the aecidia. They occur less frequently on the upper epidermis. Such an array of external hyphae would seemingly make very good respiratory organs as van Tieghem (1891) suggested for the trichogyne in *Polystigma*. However, de Bary (1887) disposed in summary fashion of that supposition and today the trichogyne of Stahl's *Collema* offers precedent for attributing a possible sexual function to these hyphae in the rusts. The tufted outgrowths also remind one of the clustered arrangement of trichogynes beneath the ostiole of the female conceptacles in *Epilithon*.

These finger-like tips of hyphae which push out through the stomata are apt to stain so densely with safranin that it is impossible to distinguish their cell contents. In the less densely stained tips a single nucleus is seen in the lower half of the finger-like hyphae. In figure 12, I have shown a series of studies of the occasional favorably stained hyphae. These are at higher magnification than the other figures. The dense nuclei or nucleoles of a, h, and left hand hypha of b and d were stained deep blue. The more diffuse nuclei, those of e and the right hand one of b stain red in a blue hypha. A more densely stained or differently stained tip can usually be distinguished on the pale-stained hyphae. This might indicate a secretion of some kind on the tip (fig. a, b). The wall usually takes the orange-G stain and such hyphae as the upper right hand one in figure e which lies at a lower plane shows merely as a pale yellow sac. There is great variation in the reaction of the hyphae to safranin and gentian violet but the more shrunken and probably older stages stain densely with safranin. Quite frequently the hypha is capped by a sphere which stains differently from the hypha. This, under favorable staining, shows a nucleus (figs. 6 and 12, a, b, c, e, f, and h). Figures 4 (right hand hypha), 7, 8, 9, and 12, g, show shrunken stages of the sphere. The profile views of 4 and 12, c and g, show a very slender connection between the sphere and the main hypha. I have arrived at no explanation of these structures, or of the red spheres of the same size that I have found occasionally on the leaf surface in the same smear with spermatia (fig. 10). Figure 12 of the hyphal tips, and figure 11, studies of spermatia taken from various groups, are drawn to the same magnification. It is to be noted that there is much variation in the size and shape of the spermatia. They are abstricted from the spermatiophores as one-celled, oval spores, and both in the spermogonium and on the surface of the leaf show a nucleus clearly in the faintly stained cytoplasm. Cases are found of elongated spores and occasionally of a binucleate condition. The older spermatia which lie in masses at the ostiole of the spermogonium and are smeared over the leaf in the spermogonial exudate

are lens-shaped bodies which stain densely with safranin. There are, here and there on the leaf surfaces, cases where a spermatium seems to have germinated. In two different lots of material from leaves fixed a month after inoculation, on which both spermogonia and aecidia are erumpent, there are spores in the spermogonial exudate which have apparently budded out hyphae. In one case the tip of a hypha from the interior of the leaf has pushed up at one side of the ostiole of a spermogonium and lies in such a mass of spores.

I have found no convincing evidences of fusion between a spermatium and one of the hyphal tips although spermatia frequently lie close to the tips. As Klebahn (1904) has remarked, there need be no special significance attached to finding masses of spermatia in the stomatal depressions on a leaf which is dotted with spermogonia.

There are many cases of binucleate cells in substomatal hyphae (figs. 3, 6 and 14). Binucleate cells are also found in the pseudoparenchyma which encloses spermogonia. These did not show in the spermogonium of which figure 2 is a detail, but their occurrence in other of the spermogonial envelopes suggests a possible connection with the hyphal tips which so often penetrate stomata close to spermogonia. Figure 15 shows a binucleate condition in runners between cells of a palisade parenchyma. The hyphae at the top of this figure are from the base of an aecidium.

The aecidial anlagen develop in the spongy parenchymatous area of the leaf. Runners from between the palisade cells pass in interlaced plectenchymatous strands between the parenchyma cells to form the main mass of the young aecidium which can be recognized even in sections where the spermogonia are only just opening. Hyphae from the lower epidermal region may also enter such an anlage. In sections where the blue-stained mycelium stands out in contrast to the yellow-stained tissue of the leaf the pattern of these hyphae may be traced in curved lines from the lower epidermis to where they make up a large part of the pseudoparenchyma of the cup. From this periphery hyphae may be traced into the base of the aecidium. By such a path, hyphae whose tips project from stomata of the lower epidermis, below an aecidial anlage, may reach the base of the anlage. I have not been able to trace this course for any one hypha but the curve figured for the terminal hypha shown in figure 5 is characteristic for hyphae in these positions. The stoma of this figure is one from a lower epidermis and the hypha is embedded in a pseudoparenchyma which completely fills the area between epidermis and the peridium of an unopened aecidium. The hypha connected with one of the tuft of hyphae shown in figure 6 was embedded in a similar mass whose cells have not been drawn in. The hyphae shown in figures 2, 3, 4, and 8 were in the near vicinity

of spermogonia. The substomatal space in these cases is much more loosely filled with hyphae. Stomata occur on both surfaces of the Oxalis leaf; spermogonia are erumpent on both surfaces; with an occasional exception, aecidia open on the lower surface. If the fertilization path is by way of hyphae which extend from tips projecting from stomata to the anlagen of aecidia one would expect the upper leaf surface to be the more favorable position for the projecting tufts of hyphae. Hyphae project upon both surfaces of the leaf but it is an index of their greater frequency on the lower epidermis that the eight examples figured on plate 4, which were chosen merely for structural details, were all from the lower epidermis.

The hyphae which push between the parenchyma cells of the leaf to form the aecidial anlagen fork repeatedly in making the felted mass at the base of the aecidium. It thus becomes very difficult to follow any one strand but the sporogenous tissue stains generally a deeper red or blue than the other cells. Binucleate cells are seen early in the very base of the aecidium (fig. 15) while among them and above them multinucleate cells also appear early in the development of the anlage. I did not find evidences of Christman fusions. There are many fusions and occasional migrating nuclei between the irregular lobes of the crowded cells. See figures 21 and 22, drawn from adjacent sections of the base of a young aecidium (fifteen days after inoculation). One is especially conscious of the third dimension in looking at sections of this stage in the aecidium. Lobes project at different planes and a slight change of focus may bring into view a new fusion. Figure 22 shows a more vacuolate cell toward the base of the aecidium and denser cells with projecting lobes above. Figure 23 from a similar young aecidium shows another multinucleate cell with a lobe which is pushing up between other cells toward the upper part of the aecidium. Allen reports that the beginnings of the spore chains appear to be lobes from the multinucleate cells. Such an origin is indicated by the figures to which I have just referred and by figure 27. The latter is figured from an older stage of an aecidium and shows the very characteristic branching which interlaces the bases of the spore chains. One is reminded here of Richard's (1896) figure for an aecidium of *Uromyces Caladii* on *Peltandra*, "showing several points of origin of the hymenium." Figures 25 and 26 also show the branching origin of spore chains. Figure 24 from an older aecidium, where the spores are formed although the aecidium is not erumpent, shows the greatly lengthened and vacuolated basal cell of a chain (de Bary's basidium). De Bary's description (1887) gives still an excellent picture of the aecidium in its three dimensions. "The hymenium now makes its appearance at the base of the aecidium, on the flat surface which abuts on the surrounding mycelium; it is composed sometimes of an irregu-

larly shaped, but much more usually of a circular and continuous layer of short cylindrically club-shaped basidia directed vertically towards the apex; each basidium abjoints a single long row of spores in basipetal succession one after another with temporary intermediate cells."

The development of the aecidium of *Aecidium punctatum* is, according to my observations, very similar to that of *Puccinia Sorghi*. In the aecidium binucleate cells occur regularly in the basal tissue. There are instances here also of migrating nuclei. I have not, however, found this in the higher region of the basal cells of spore chains. The spermogonia of *Aecidium punctatum* are subcuticular. In their formation, hyphae push up between the epidermal cells and grow in the cutin toward a common point. In sections of spermogonia the remnants of these closely woven hyphae can be seen in the red-stained cutinous cap over the hemispherical spermogonium. There are few paraphyses and these slant as a thatch toward the top of the spermogonium. Under this thatch from a layer of basal cells just outside the host epidermis an upright growth of spermatiophores develops. The spermatia which are successively abstricted, discharge in great numbers through the central hole in the thatch of paraphyses. The latter do not project from this ostiole. Spermatia are found abundantly in the sections, on the surface of the leaves but, since the amphigenous stomata of the Hepatica leaf are not located in depressions as in Oxalis, there is no particular massing of spermatia around stomata. In this rust hyphae do not project through stomata according to my observations. In comparison with *Puccinia Sorghi* the absence of any projecting tufts is marked on sections of leaves containing spermogonia and aecidia of approximately the same age as those of Oxalis from which figures 2–12 were made. I did find, however, many instances of hyphal tips just below or within the stoma (fig. 19) and of hyphal tips which had pushed up between epidermal cells and run horizontally in the cutin. A binucleate condition is frequent in these cells. Binucleate cells and migrating nuclei are found in the mycelium around the spermogonia.

DISCUSSION

As reported above, I have found in *Puccinia Sorghi* upon *Oxalis* much the same structures which Allen (1932) reports for *Puccinia triticina* upon *Thalictrum*. These hyphae which push out through stomata may be trichogynes, but I lack the proof of fusions between these hyphae and spermatia. Except for Craigie's evidence that spermatia function in the production of aecidia and for our further knowledge of nuclear distribution in the hyphal cells, the matter stands as it did in the time of de Bary when he considered the evidence was insufficient to warrant calling the hyphae

trichogynes. The hypothesis offers another possible explanation for the substomatal hyphae which Clinton (1919) describes for *Cronartium ribicola* in the needles of *Pinus Strobus*. Clinton believes that sporidia of this rust, contrary to the usual habit of sporidia, enter through the stomata of the host. He has not found the entering germ tubes but he finds, in substomatal spaces of infected leaves, a vesicle from which a hypha leads to the intercellular spaces and from which a short beak projects between the guard cells. He considers the vesicle "to be an inflation of the germ tube immediately it has passed the guard cells into the air chamber" but in his figure 6, plate 43, the hypha is sufficiently like some which I have found to suggest that it might be growing out instead of in. Clinton, however, does not report any binucleate hyphae and he finds no trace of penetrations through epidermal cells as I have in Oxalis. The fact that these hyphae in the case of *Aecidium punctatum*, do not appear to push out through stomata but directly between epidermal cells, need not necessarily be evidence against their functioning as trichogynes. The binucleate hyphae between epidermal cells and in the cuticle may serve this same function but this difference in structure and habit should make one realize that there is much yet to be seen before we may talk confidently of trichogynes in connection with the rusts.

I did not find the multinucleate condition in trichogyne-like cells, as reported by Allen (1932) for *Puccinia triticina*, in any of the rusts which I investigated but until further observations are available it is perhaps unnecessary to consider this point further. In the matter of the aecidial anlage there is also need of much more observation. Conditions observed in *Puccinia triticina* and in *Puccinia Sorghi* certainly suggest that the nuclear conditions reported by earlier workers as abnormalities or exceptions to the method of the initiation of spore chains by the Blackman or Christman types of fusion are to be further studied.

The reports which I have seen in the literature, of Blackman and Christman fusions made by sixteen workers from 1904 to 1927 show fusions for nineteen rusts of the caeoma type and twenty-four of the peridium type. One cannot therefore regard the phenomenon as a caeoma type character even though it is in the peridium type that recent investigators fail to find them. The figures from these publications vary greatly in the value of their evidence for fusions. Several of the students in this list mention the apparently sporadic occurrence of binucleate cells below the fusion cells. Allen lists five instances of sporophytic mycelium mingled with gametophytic as reported in the literature. The earliest is that of Blackman and Fraser who report that in *Puccinia Poarum* "paired nuclei were also to be observed at a stage before the differentiation of the fertile layer

or in cells below that layer after its differentiation." It may be that these cases are really nothing more than the early occurrence of binucleate cells which I found to be a regular occurrence in both Oxalis and Hepatica rust.

Andrus (1931) mentions cases in the bean rust where nuclei were found passing through the cross walls of hyphae which enter the aecidium and migrating into the fertile cells of the aecidium. He interprets this as an evidence of fertilization from trichogenous hyphae above. The matter is of course conjecture at present but it is open to question whether these cases may not be part of the cell fusion phenomenon which I have found, in the Oxalis rust, linked up apparently with the occurrence of multinucleate cells. The cases of nuclear migration which I found in both Oxalis and Hepatica rust were located in the base of the aecidium.

Allen (1930, 1932) does not discuss the possibility that the multinucleate cells of the young aecidium may arise by cell fusions. Such an occurrence would have at least the support of comparative morphology. The formation of coenocytic cells by fusions is a part of the post-fertilization process in the development of carpospores in the red algae. The Christman fusions have been compared by Dodge (1926) to the auxiliary cell fusions in the red algae. *Dudresnaya,* upon the authority of Oltmanns (1922), is now a classic case for successive fusions between gonimoblasts and auxiliary cells. For comparison with the aecidial fructification the isolated carposporic masses of *Dudresnaya,* which arise where each new length of gonimoblastic filament fuses with an auxiliary cell, may be telescoped into one fruit. This condensation of many cystocarps into a single conceptacle occurs in the Corallinaceae. In this group antheridia, carpospores and tetraspores all develop as aggregates in conceptacles. Nichols (1908) has described the process of carpospore formation in certain Corallines of the Pacific coast. Although he gives no cytological data he describes and figures the carpospores in the cystocarpic conceptacle for three species of *Lithophyllum* and for *Lithothamnium marginatum* as arising from a large coenocytic basal cell. He writes: "A disk-shaped placenta occupies the base of the conceptacle around the periphery of which the carpospores occur." Kylin (1928) traces the development of the cystocarpic conceptacle in *Epilithon membranaceum* showing that it involves the formation of a gigantic coenocytic cell by the fusion of gonimoblasts and auxiliary cells. From the floor of the young conceptacle rows of upright cells arise. In the central group are three-celled carpogonial branches, tipped with trichogynes. Around them stand two-celled auxiliary cell branches. After fertilization the carpogonium fuses with the first cell of a carpogonial branch but not necessarily with a cell of its own branch. From the resulting fusion cells gonimoblasts develop which fuse with basal cells of the aux-

iliary branches. Kylin concludes: "Im Schlussstadium beobachtet man indessen, dass alle Auxiliarzellen und Nährzellen, sie mögen in den Karpogonästen oder in den Auxiliarzellästen auftreten, miteinander zu einer grossen Fusionszelle verschmolzen sind . . . Aus dem Rande der Fusionzellescheibe entwickeln sich mehrere zwei-bis dreizellige Fäden, deren oberste Zellen Karposporen bilden."

Surely this multinucleate cell may serve as a prototype for aecidial development in which multinucleate cells are reported in the primordium, yet Allen does not discuss this possibility.

The nuclear problem, however, is by no means solved by an *Epilithon* prototype. The behavior of the nuclei in the red algae with the nucleus of the auxiliary cell remaining in the far corner of the fusion cell and the diploid nucleus alone continuing in gonimoblasts and carpospores seems clear on an Oltmann chart for *Dudresnaya* or *Calithamnion*. Still the nuclear behavior has not been worked out for *Epilithon*. A confirmation of Oltmann's (1922) claim as to the fate of the auxiliary cell-nuclei is very much needed.

The evidence brought by Rosenvinge (1929) that in *Phyllophora Brodiaei* the reduced sporophyte is in permanent nutritive relations with the haploid gametophyte might indicate an extension of such a purely nutritive function of auxiliary cells with the disappearance of the diploid carposporic stage. Rosenvinge reports for this species that although there are antheridia and procarps on the same plants no spermatia are seen upon the aborted trichogynes and there are no other signs of fertilization. Nevertheless the "bearing cell" at the base of the procarp, originally uninucleate, becomes plurinucleate and sends out protuberances. These force their way between the cells of the gametophytic tissue but instead of developing carpospores as do the gonimoblasts of the related species, *Phyllophora membranifolia*, they form, on this gametophytic plant, low, wartlike structures similar to the nemathecia of the diplobiontic *Phyllophora membranifolia* and, as it would seem to me, morphologically comparable to the uredo-teleuto mycelium and spores in the rusts. Here again Ruth Allen (1930) might have found a suggestive similarity with the multinucleate cells of the aecidium as they "push down into the sterile 'space-making' tissue of the aecium to produce spore chains." In the nemathecium, within an outer portion of radiating filaments, there is a medullary tissue of rounded cells which develop typical tetraspores. The nuclear condition of the tetraspores has not been investigated but it is seemingly complicated by connections between fertile cells in contiguous rows as well as the usual ones within each row. Rosenvinge remarks "It would be of interest to study the fate of the migrating nuclei in this process."

Rosenvinge has germinated these tetraspores of the nemathecia and obtained from them small thalli which resemble young stages of *Phyllophora Brodiaei*. The nemathecia are thus proved to be part of the life-cycle of *Phyllophora* rather than a parasite. Rosenvinge states that a closer cytological investigation needs to be made but he believes that in this species the carposporophytic phase has disappeared and in its place a tetrasporophyte is developed whose vegetative part is only represented by the intramatrical cell-filaments imbedded in the haploid tissue of the parent gametophyte. The importance of this simplified condition of the sporophyte lies in the fact that *Phyllophora* belongs to that group of the red algae which Svedelius (1931) calls the *Polysiphonia* type: a typical diplobiont with morphological alternation of generations and reduction division at the time of tetraspore formation. The shortening of the diploid generation without losing the advantage of multiplication by spores as seen here is, Svedelius (1931) thinks, carried to a climax of simplification in *Ahnfeltia plicata* where, as reported by Rosenvinge (1931), nemathecia are the only reproductive organs known. Rosenvinge has followed the development of these spores and emphasizes their multiple origin from a layer of generative cells in the nemathecium. He thinks that these generative cells may be reduced procarps and that the whole complex of cells arising from the generative cells must be considered as representing a new generation comparable to the sporophytic generation in *Phyllophora Brodiaei*. This theory raises questions concerning nuclear conditions and chromosome numbers which require further cytological work but it certainly suggests a comparison with the multiple origin of the aecidiospore chains in the aecidium cup.

There are cases among the reduced Ascomycetes which parallel closely the conditions in the autotrophic *Phyllophora*. We have cases, where, as reported by Fraser, there is a degeneration of sexual organs and, consequently no fertilization but where the asci still develop. In *Lachnea stercorea* (Fraser, 1907) although the antheridium fuses with the trichogyne its contents are said not to travel to the oogonium. Nevertheless the nuclei of the oogonium increase in number, fuse in pairs and these fusion nuclei supply the ascogenous hyphae. In *Lachnea cretea* (Fraser, 1913) there is a branched trichogyne but no antheridium has been observed. Nevertheless, in the central part of the archicarp the septa break down and ascogenous hyphae arise from the resulting multinucleate fusion cell. In *Humaria rutilans* (Fraser, 1908) reduction has gone still further; sexual organs are completely lacking and ascogenous hyphae arise from cells which contain fusion nuclei. There seems to be a parallelism in the basic facts of spore development between the rusts, the Ascomycetes, and their possible an-

cestors, the red algae. If functioning trichogynes as well as spermatia are now to be looked for in the rusts one may expect to find a *Polysiphonia* type, but there are many variants to be fitted in.

Dodge (1924) has reported three races of the short cycled form of *Caeoma nitens:* one a male race with spermogonia but with uninucleated aecidiospores producing two-celled promycelia; second, a female race with spermogonia lacking and uninucleated aecidiospores producing two-celled promycelia; a third hermaphroditic race with spermogonia present and binucleated aecidiospores producing four-celled promycelia. Dodge (1932) has described these as "androgenetic, parthenogenetic, and syngamic (hermaphroditic) races." With the steps in the process which initiates the sporophytic generation in the rusts still not clear, there is, nevertheless a possible parallelism between the hermaphroditic race of *Caeoma nitens* and *Phyllophora Brodiaei*, and between the uninucleate races of *Caeoma nitens* and the simplified type of *Ahnfeltia plicata.*

Suggestive as such comparisons are as a help toward explaining reproductive processes in the rusts it should be remembered that the nuclear problem, (assuming that Oltmann's account of the nuclear behavior in the so-called secondary and tertiary fertilizations of *Dudresnaya* is true), is a very different one in the rusts as compared with the red algae and the other great parasitic group, the Ascomycetes. In the rusts conjugate nuclei are the accepted fact of the diploid generation. The rusts belong, moreover, to the line of Basidiomycetes which, by means of the clamp connection mechanism, insures the perpetuation of a line of non-sister nuclei. Thus comparisons with the red algae where the diploid nucleus is so far as known, single, as compared with the rusts where conjugate nuclei are present in the diplont; and with the Ascomycetes where the crozier offers a still different method for sorting out nuclei still leave many problems to be cleared up.

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Description of plates 4–6

The figures of plates 4–6 were drawn with the aid of a camera lucida from sections 5–7.5 microns thick. For figs. 1–9 and 13–27 a Zeiss apochromatic objective 4 mm. and compensating ocular 15× were used, with approximate magnification ×1200; for figs. 10–12 a 1/16 inch oil immersion objective and an ocular 15× were used, with approximate magnification ×1800. The following fixations were used:

Figs. 16–20	Flemming's medium solution
Figs. 12g, 19, 24, 25	Flemming's weak solution
Figs. 1, 3, 4, 8–10, 12e, 13–15, 21, 22, 27	Allen's B-15 solution
Figs. 6, 12a–d, f, h, 26	Carnoy's solution
Figs. 2	50% alcohol
Figs. 5, 7	Corrosive sublimate in 70% alcohol

The material was stained in Flemming's triple stain.

PLATE 4

Puccinia Sorghi in *Xanthoxalis stricta*

Fig. 1. An infection hypha in a cell of the upper epidermis near a spermogonium.

Fig. 2. Short branches from hyphae at the border of a spermogonium, projecting from a stoma of the lower epidermis.

Fig. 3. A hyphal tip protruded from a stoma. Binucleate hyphae in the substomatal space.

Fig. 4. A group of hyphae at a stoma showing their independent origin from substomatal hyphae. The external depression in which the stoma lies is filled by a mass of spermatia in the spermogonial exudate.

Fig. 5. A hypha lying in a mass of pseudoparenchyma which fills the space between lower epidermis and an aecidium. The tip of the hypha projects against a guard cell of a stoma.

Fig. 6. A tuft of hyphae projecting from a stoma. The dense hyphae are stained red, the others are pale blue with deep blue nuclei. The pseudoparenchyma in which the substomatal hypha is embedded has been omitted. The hypha extends in the direction of an aecidium.

Fig. 7. A shrunken, blue-stained hyphal tip which has pushed out between companion cell and guard cell of a stoma; in the same microscopic field as fig. 5.

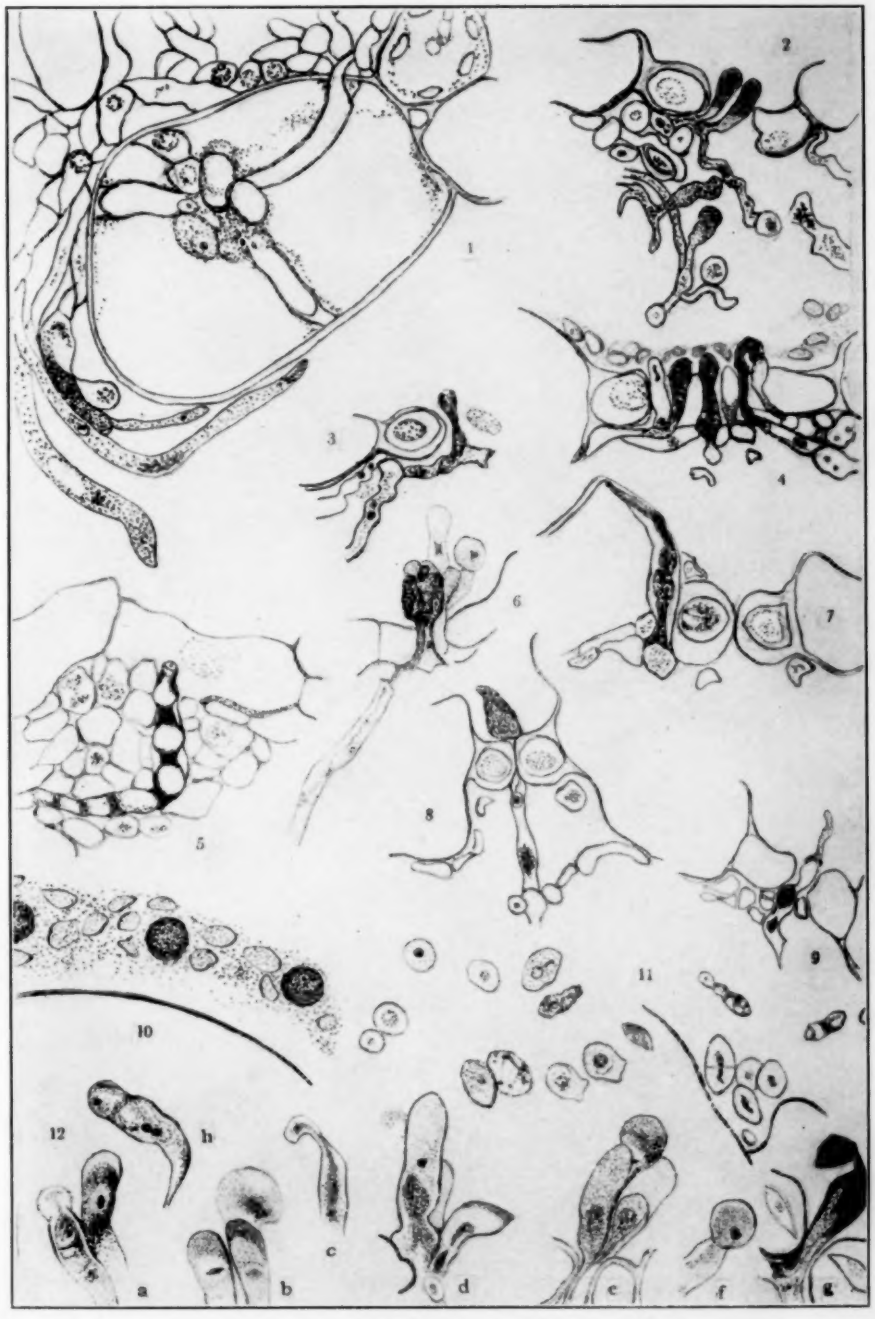
Fig. 8. A substomatal hypha with a dense, red-stained tip projecting above a stoma into the depression between the two companion cells. The stoma is near a spermogonium.

Fig. 9. A shrunken hyphal tip projecting from a stoma; from the same section as fig. 8 but below an aecidium.

Fig. 10. Red-stained spheres in a smear of spermatia upon a leaf surface; near the tuft of projecting hyphae shown in fig. 12, e.

Fig. 11. Spermatia drawn from groups found on the leaf surfaces in the vicinity of spermogonia. The dense nucleus at the upper left is red-stained; the others are blue. The three at the upper right are of the type from which, in three cases, germinating hyphae had issued. These were found each time in spermatial masses at the ostioles of spermogonia.

Fig. 12. Tips of hyphae which protruded through stomata; drawn to the same magnification as figs. 10 and 11.



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a. A group from a hypha on the same epidermis as fig. 6.

b. A group from thes ame section as fig. 12, a. The hyphae are stained blue; the left hand nucleus, blue, and the right hand nucleus, red. The terminal sphere is stained yellow with red contents.

c. Detail of the hypha which is at the lower plane in fig. 12, d. A terminal sphere is shown in profile.

d. Another group from the same section as fig. 6.

e. A group of hyphae from the same section as figs. 8 and 9. Two pale yellow hyphae which lay at an upper level have been omitted from the figure.

f. Enlargement of right hand hypha from fig. 6.

g. An old hypha with dense, red-stained contents and profile view of a spherical tip. Both aecidia and spermogonia are near the stoma.

h. A hypha from a stomatal group from the same section as fig. 6.

PLATE 5

Puccinia Sorghi in *Xanthoxalis stricta*

Fig. 13. Paraphyses and protruding hyphae at the ostiole of a spermogonium.

Fig. 14. A hypha with binucleate cells in a substomatal space.

Fig. 15. Binucleate hyphae between palisade cells. The hyphae in the upper part of the figure are in the anlage of an aecidium.

Puccinia Violae in *Viola cucullata*

Fig. 16. Binucleate hyphae in front of a guard cell of a stoma on the upper epidermis: possible infection hyphae from aecidiospores.

Fig. 17. Binucleate hyphae at a stoma in another section of a violet leaf.

Fig. 18. A short hyphal branch protruding from a stoma. The cell below is a cross section of the runner from which the hypha arises.

Aecidium punctatum in *Hepatica acutiloba*

Fig. 19. A substomatal hypha with its tip between two guard cells.

Uromyces Caladii in *Arisaema triphyllum*

Fig. 20. A terminal hypha in a stoma. A spermatium lies at the surface of the guard cell.

PLATE 6

Puccinia Sorghi in *Xanthoxalis stricta*

Fig. 21. Detail from the base of a young aecidium in a 15 day-old infection.

Fig. 22. Detail from the next section of the same aecidium as that of fig. 21.

Fig. 23. Multinucleate cells from a young aecidium.

Fig. 24. A "basidium" from an aecidium in which the spore chains are formed.

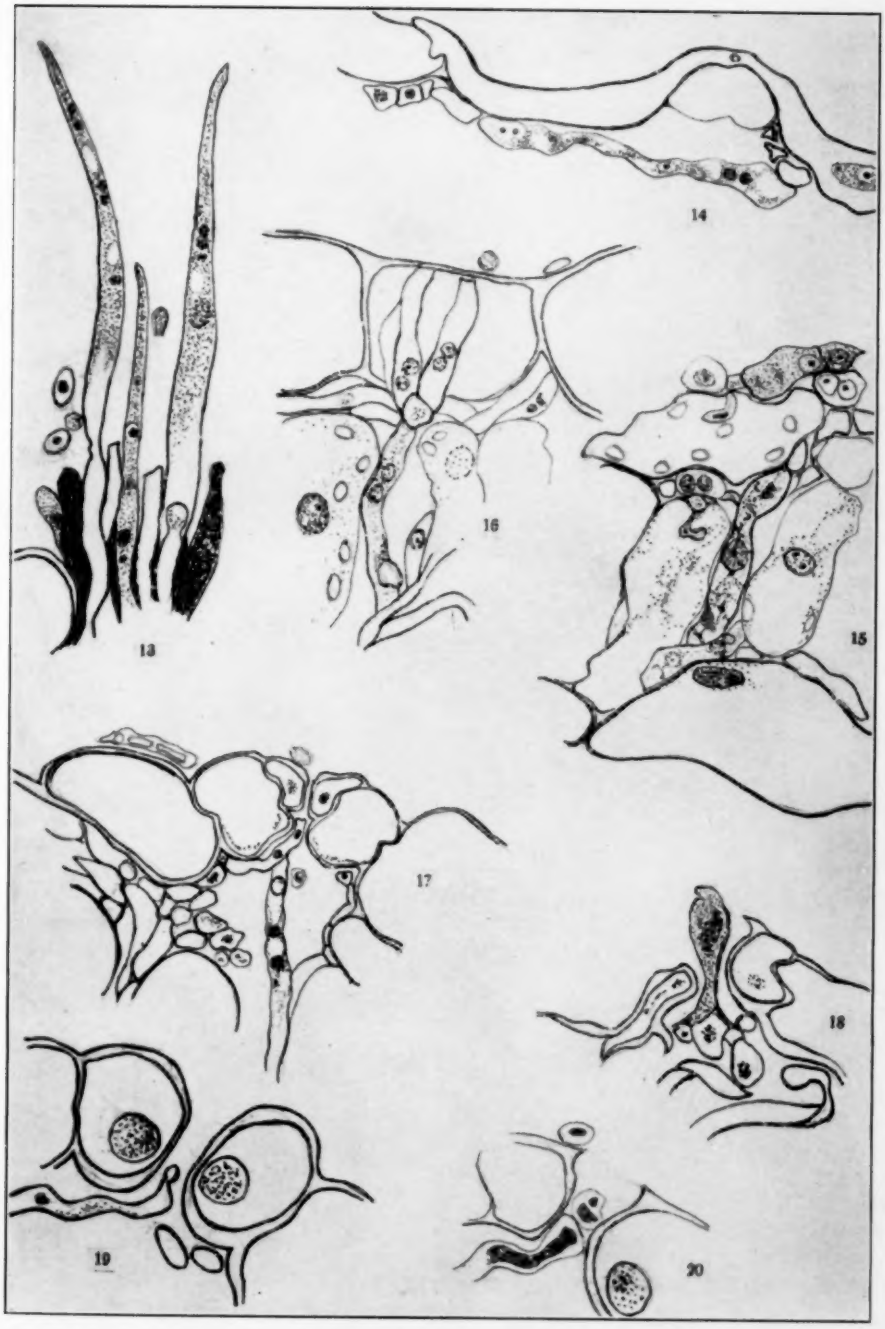
In figs. 21–24 the upper part of the figure is toward the upper surface of the leaf. The aecidium is developing toward the under surface.

Fig. 25. An intermediate stage between figs. 23 and 24, showing branching origin of spore chains.

Fig. 26. A stage of the "basidium" younger than that of fig. 24.

Fig. 27. Vertical section of the anlage of an aecidium.

In figs. 25–27 the position of the cells is the reverse of figs. 21–24.



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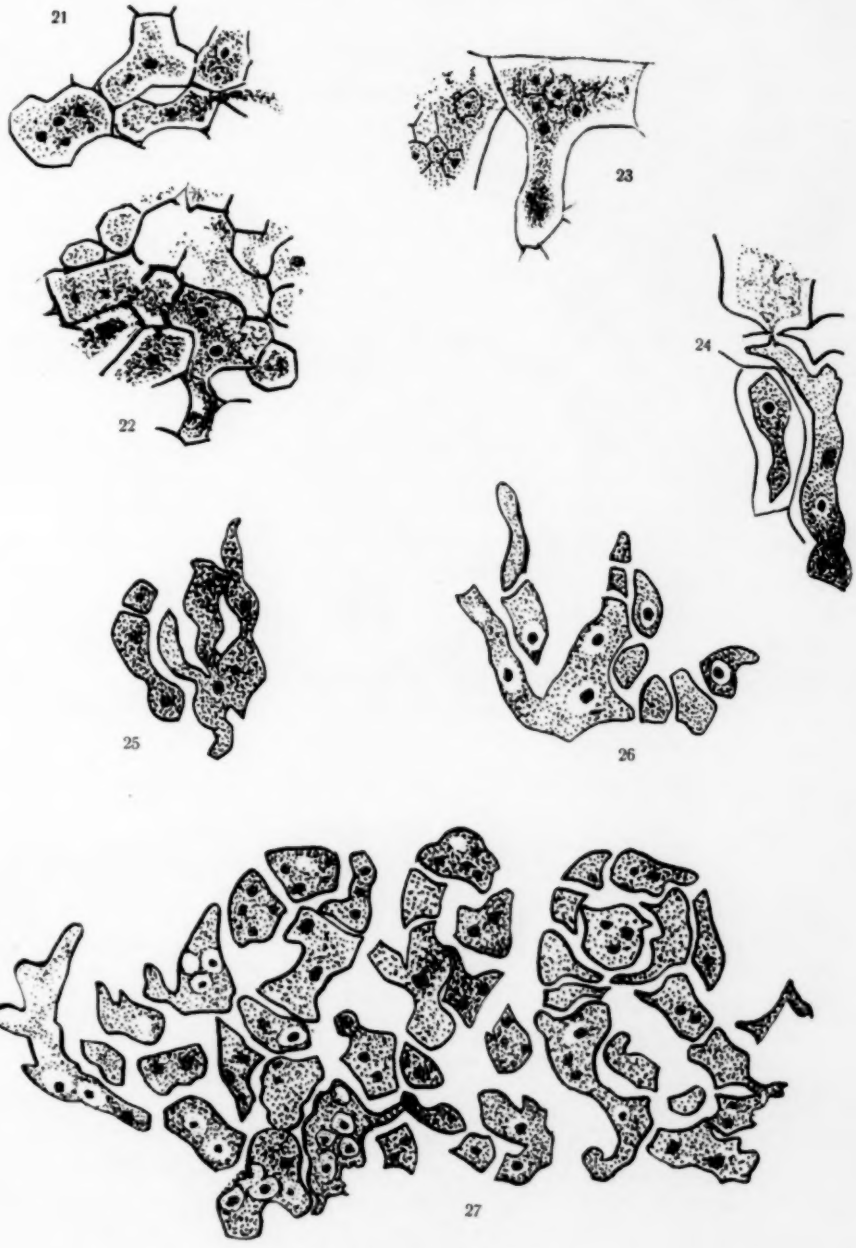

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Nomenclatural notes

HAROLD N. MOLDENKE

Callicarpa Merrillii Moldenke, nom. nov.

In reviewing the literature on the verbenaceous genus *Callicarpa* in connection with a monograph of the American members of this genus which is at present in preparation, it was discovered that the name *Callicarpa lancifolia* proposed by Merrill in 1915 (Philipp. Jour. Sci. Bot. 10: 70) for a new Philippine species of this genus, is a homonym of the earlier *C. lancifolia* Millsp. (Publ. Field Columb. Mus. Bot. 2:312.1909) and is therefore invalid. The Philippine species, the type of which was collected by Maximo Ramos (Philipp. Bur. Sci. No. 11,078) on the island of Cebu in March, 1912, must therefore be given a new name, and for it the new binomial *Callicarpa Merrillii* is hereby proposed. It is indeed most fitting and proper that this specific name be applied to the plant in question, in commemoration of Dr. Elmer Drew Merrill, who first recognized it as a new species, and who has done such extremely noteworthy work on the Asiatic flora and more especially on that of the Philippine Islands. *C. Merrillii* is apparently closely related to *C. stenophylla* Merr. and *C. longifolia* Lam., and is known also from the islands of Mindoro, Ticao, Mindanao, and Basilan. The type of *C. lancifolia* Millsp., on the other hand, was collected by Charles Wright (No. 3173) in eastern Cuba between the years 1860 and 1864. The latter—a very distinctive and endemic Cuban species—will be fully discussed in the writer's forthcoming monograph.

CALLICARPA NUDIFLORA Hook. & Arn.

It has also been found through a study of the literature on this extremely interesting genus that the Asiatic plant hitherto known as *C. acuminata* Roxb. must take on a new name. It is true that the name *C. acuminata* was first proposed by Roxburgh for this Asiatic species (Hort. Beng. 10. 1814), but without any description. Being therefore a hyponym, it was not validly published at this date. A full description of his *C. acuminata* was not published by Roxburgh until 1820 (Fl. Ind. 1:394). In the meantime, however, Humboldt, Bonpland, and Kunth published their Central and South American *C. acuminata* (Nov. Gen. & Sp. Pl. 2:252. 1817) and accompanied the name with a full description. The Asiatic and American plants are not conspecific. The American plant, therefore, must retain the name *C. acuminata* H.B.K. given to it in 1817 because Roxburgh's use of the name in 1814 was not valid publication; and Roxburgh's Asiatic species must take on a new name. The second oldest name for this Asiatic species is *C. Reevesii* of Wallich (Cat. no. 1830. 1829), but

this also is a mere hyponym. The name *C. Reevesii* Wall. was not validly published until by Walpers in 1845 (Rep. Bot. Syst. 4:125). In 1836, however, Hooker & Arnott published *C. nudiflora* (Bot. Beech. Voy. 206) with a good description and illustration. It is therefore obvious that this Asiatic species first known as *C. acuminata* Roxb. and then as *C. Reevesii* Wall. must now be called *C. nudiflora* Hook. & Arn. It has been collected rather extensively in south China, Canton, Kwantung, Hainan, Macao, and Lappas Island, and occurs also in Silhet, Tenesserim, and Singapore.

Celeri graveolens var. **dulce** (Mill.) Moldenke, comb. nov.

Celeri graveolens var. **rapaceum** (Mill.) Moldenke, comb. nov.

The generic name *Celeri* of Adanson (Fam. Pl. 2:498. 1753) is maintained by Britton and others for the six or more species of *Apium* which are characterized by having white flowers and oval fruit. The true genus *Apium*, then, according to this view, is limited to the twenty or more species with yellow flowers and hemispheric fruit. Since the genus *Celeri* has thus been accepted, with the common celery (*Apium graveolens* L.; *Celeri graveolens* [L.] Britton) as the type species, it is obvious that the two common garden varieties of this species known respectively as the upright celery and the celeriac must likewise be transferred to this genus. The combination *Celeri graveolens* var. *dulce* is therefore hereby proposed for the *Apium dulce* of Miller (Gard. Dict., ed. 8, no. 5. 1768)—a plant which has likewise been called *Apium Celeri* by Gaertner (Fruct. & Sem. 1, t. 22. 1788) and *Apium graveolens* var. *dulce* by De Candolle (Prodr. 4:101. 1830)—and the combination *Celeri graveolens* var. *rapaceum* for the *Apium rapaceum* of Miller (Gard. Dict., ed. 8, no. 6. 1768), which is the *Apium graveolens* var. *rapaceum* of De Candolle (Prodr. 4:101. 1830).

Cynoxylon floridum var. **pendulum** (Dipp.) Moldenke, comb. nov.

Cynoxylon floridum var. **rubrum** (André) Moldenke, comb. nov.

Since the flowering-dogwoods, which are distinguished by being trees or shrubs with capitate flowers involucrate by four large white or colored bracts, are by many modern authorities kept distinct, as the genus *Cynoxylon* Raf. (Alsog. Amer. 59. 1838), from the ordinary dogwoods or cornels which make up the genus *Cornus* L. (Sp. Pl. 117. 1753) proper and which are distinguished by their cymose and non-involucrate inflorescence, then it is obvious that the two common horticultural varieties known respectively as the weeping flowering-dogwood and the red flowering-dogwood must be renamed. Being varieties of the *Cornus florida* of Linnaeus which is now more properly called *Cynoxylon floridum* (L.) Raf., they also must be transferred to the genus *Cynoxylon*. This has apparently not been

done up to the present time. The combination *Cynoxylon floridum* var. *pendulum* is therefore hereby proposed for the *Cornus florida* var. *pendula* of Dippel (Handb. Laubh. 3:244. 1893) and the combination *Cynoxylon floridum* var. *rubrum* for the *Cornus florida* var. *rubra* of André (Rev. Hort. 66:500. 1894).

Pleuropterus sachalinensis (F. Schmidt) Moldenke, comb. nov.

The name *Pleuropterus* was proposed as a genus of the *Polygonaceae* by Turczaninow in 1848 (Bull. Soc. Nat. Mosc. 21[1]:587). Recent workers on this family, like Steward, have reduced the name to sectional rank under the genus *Polygonum* or have united it with *Tiniaria*, while others, like Small and Nakai, have retained it as a valid genus. The characters distinguishing members of the genus *Pleuropterus* from all other members of the *Polygoneae*, as given by Small in a key to genera in Britton & Brown's "Illustrated Flora" (ed. 2, 1:647. 1913), are as follows: Plants with fibrous roots or slender rootstocks, without scaly caudices; stems branching; leaves not basal, their blades not jointed; ocreae oblique, not 2-lobed, but more or less open on the side facing the leaf; inflorescence branched; sepals, at least the outer ones, keeled or winged; filaments slender; stigma dilated, toothed; styles divaricate. In the opinion of the present writer, *Pleuropterus* ought certainly be retained as a valid genus, since its members are so distinct in their technical characters and in their habit and general appearance and are so easily recognized. The *Polygonum sachalinense* of F. Schmidt (Maxim., Prim. Fl. Amur. 233. 1859), then, must be transferred to this genus. The name *Pleuropterus sachalinensis* is therefore hereby proposed for this plant. This genus, then, to date contains four species, all natives of eastern Asia, although the second is locally naturalized in the eastern United States: (1) *Pleuropterus multiflorus* (Thunb.) Turcz.—first named *Pleuropterus caudatus* by Turczaninow and made the type of the genus, but since this name was confessedly only a new binomial for the *Polygonum multiflorum* of Thunberg (Fl. Jap. 1:169. 1784) it was later corrected by Turczaninow himself to *Pleuropterus multiflorus* (vid. Nakai in Fedde, Repert. 13:267. 1914), which, obviously, is the name which will have to be adopted for this species; (2) *Pleuropterus Zuccarinii* Small (in Britton & Br. Ill. Fl., ed. 2, 1:676. 1913); (3) *Pleuropterus ciliinervis* Nakai (in Fedde, Repert. 13:267. 1914); and (4) *Pleuropterus sachalinensis* (F. Schmidt) Moldenke (the *Polygonum sachalinense* of F. Schmidt).

Viorna albicoma (Wherry) Moldenke, comb. nov.

Since the thirty or more species of leatherflowers, which are characterized by their erect or ascending stems, their mostly solitary flowers, and

their more or less converging sepals, are usually kept distinct as the genus *Viorna* of Reichenbach (Handb. 277. 1837)[1] from the approximately similar number of species of virginsbowers which compose the true genus *Clematis* of Linnaeus (Sp. Pl. 543. 1753), and which are distinguished from the above by their spreading sepals and stamens and their panicled flowers, then the *Clematis albicoma* of Wherry (Jour. Wash. Acad. Sci. 21:198, *fig. 1.* 1931) must be transferred to this genus. The combination *Viorna albicoma* is therefore hereby proposed for this rare Virginian and West Virginian plant.

Vitex tomentulosa Moldenke, sp. nov.

Frutex; ramulis gracilibus obtuse tetragonis densissime et breviter brunneo-tomentulosis glabrescentibus; internodis valde abbreviatis; cicatricibus foliorum delapsorum plerumque conspicuiter impressis; foliis oppositis trifoliolatis; petiolis gracillimis densissime et breviter tomentulosis; petiolulis ad 1 mm. longis vel nullis dense tomentulosis; foliolis 3, medio subcoriaceo anguste lanceolato longe acuminato revoluto ad basin cuneato et in petiolulum attenuato, supra minutis resinosis globulis vel lepidibus dense obtecto, subtus densissime brunneo-tomentuloso; foliolis lateralibus medio consimilibus sed paulum parvioribus; inflorescentiis axillaribus paniculatis; pedunculis gracillimis densissime et breviter tomentulosis; cymis ut videtur in quaque panicula 5 parvis, infernis oppositis, quoque jugo a bracteis linearibus 2 subtento; bracteis utrinque dense tomentulosis; bracteolis et prophyllis numerosis linearibus tomentulosis; calicis obconico-campanulati plusminus 4–5-angulati densissime granuloso-pulverulenti limbo subtruncato ad apicem angularum vix vel paulo 4–5-dentato; corollae infundibulariformis vel hypocrateriformis tubo late cylindrico intus plusminus dense piloso, lobis 4 oblongo-lingulatis paulum inaequalibus latissime rotundatis puberulentibus, extra leviter granuloso-pulverulentis; staminibus 4 prope os tubae corollae insertis; filamentis pilosis; stylo glabro; stigmate bifido.

Shrub; branchlets rather slender, grayish, obtusely tetragonal, very densely short-tomentulose with brownish tomentum, becoming glabrate in age; internodes much abbreviated, usually 4–6 mm. long at the tips of the branchlets; leaf-scars usually conspicuously impressed; leaves decussate-opposite, trifoliate; petioles very slender, 2.5–5.5 cm. long, flattened and conspicuously canaliculate above, very densely short-tomentulose; petiolules extremely short (or absent), to 1 mm. long, flattened and deeply canaliculate above, densely tomentulose; leaflets 3, the terminal one subcoriaceous, narrow-lanceolate, 4–6.5 cm. long, 8–15 mm. wide, long-acuminate at apex, revolute along the margins, cuneate at the base and attenuate into the petiolule, densely covered with minute resinous globules or scales above, less so in age,

[1] This name was apparently first proposed [as a section of *Atragene*] by Persoon in his "Synopsis Plantarum" (part 2, p. 98. 1807). The generic name is on this account inaccurately accredited to him by Reichenbach.

very densely brownish tomentulose beneath with extremely short appressed scurfy tomentum; midrib deeply impressed above, very prominent beneath; secondaries about 8 pairs, short, ascending, impressed above, prominent beneath; lateral leaflets similar in all respects to the terminal one only slightly smaller; inflorescence axillary, paniculate, 3–5 cm. long (in bud); peduncles very slender, 1.5–3 cm. long, very densely short-tomentulose; cymes apparently about 5 in each panicle, small, the lower ones paired, to about 1 cm. long, each pair subtended by 2 linear bracts which are to 1 cm. long and densely tomentulose on both surfaces; bractlets and prophylla numerous, linear, tomentulose; calyx obconic-campanulate, about 2.8 mm. long and 2.6 mm. wide, somewhat 4–5-angled, subtruncate, scarcely or very slightly 4–5-toothed on the angles, very densely granulose-pulverulent; corolla infundibular or hypocrateriform, its tube broadly cylindric, about 2.3 mm. long, very much ampliate above, more or less densely pilose within, its limb 4-parted, slightly irregular, its lobes broadly oblong-lingulate, 1–1.3 mm. long and wide, very broadly rounded at apex, puberulent, slightly granulose-pulverulent on the back; stamens 4, inserted near the mouth of the corolla-tube; filaments filiform, about 1.3 mm. long, pilose; anthers oblong, about 0.6 mm. long and 0.3 mm. wide; style capillary, 2–3 mm. long, glabrous; stigma bifid, its branches about 0.5 mm. long, erect, somewhat divergent; ovary subglobose, about 0.7 mm. long and wide, somewhat tetragonal, granulose-pulverulent on the top; fruiting-calyx and fruit not seen.

The type of this interesting species was collected by A. Fors [*Juan T. Roig 5831*] at Los Yayales Remates de Guane, Pinar del Rio, Cuba, on March 25, 1929, and is deposited in the herbarium of the New York Botanical Garden. A vernacular name for this plant, according to its collector, is "Robleguiro." The species is very distinct and quite different from all other known West Indian species.

Xanthoxalis corniculata var. **atropurpurea** (Planch.) Moldenke, comb. nov.

Since the generic name *Xanthoxalis* of Small (Fl. SE. U. S. 666. 1903) is now applied to the fifty or more species of yellow-flowered caulescent woodsorrels, the common horticultural variety known as the purple-leaved yellow woodsorrel must likewise be transferred to this segregated genus. The combination *Xanthoxalis corniculata* var. *atropurpurea* is therefore hereby proposed for the *Oxalis corniculata* var. *atropurpurea* of Planchon (Fl. Serres 12:47. 1857). This variety has been found by the present writer to persist quite extensively after cultivation and often becomes quite weedy. It will frequently be met with as an escape around old gardens and in waste ground.

The New York Botanical Garden

INDEX TO AMERICAN BOTANICAL LITERATURE
1930–1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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